

***Pseudopodoces humilis*, a misclassified terrestrial tit (Paridae) of the Tibetan Plateau: evolutionary consequences of shifting adaptive zones**

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Pseudopodoces humilis (Hume's Ground-Jay) is a small passerine bird that inhabits the high rocky steppes of the Tibetan (Qinghai–Xizang) Plateau. Although it was long classified as a small species of ground jay (*Podoces*), two previous anatomical studies cast doubt on its assignment to the Corvidae (crows and jays). We studied the evolutionary relationships of *Pseudopodoces* using three independent datasets drawn from comparative osteology, the nuclear *c-myc* gene, and the mitochondrial cytochrome *b* gene. All three datasets agree on the placement of *Pseudopodoces* in the family Paridae (tits and chickadees). The cytochrome *b* data further suggest that *Pseudopodoces* may be closest to the Great Tit *Parus major* species group. *Pseudopodoces* is the only species of parid whose distribution is limited to treeless terrain. Its evolutionary relationships were long obscured by adaptations to open habitat, including pale, cryptic plumage; a long, decurved bill for probing in crevices among rocks or in the ground; and long legs for terrestrial locomotion. Despite these accommodations to a novel adaptive zone, its evolutionary affinity with the Paridae is clearly expressed in comparative osteology and genetics, and is supported by its habit of nesting in cavities.

Tits and chickadees (family Paridae) are frequently chosen as study subjects in field ornithology, partly because they are ubiquitous songbirds in Holarctic forests and woodlands, cavity-nesters that often accept nestboxes, and year-round residents over most of their range. In recent years, articles that address the genus *Parus* have appeared at a rate of at least 100 per year (see *Biological Abstracts*, published by BIOSIS, Philadelphia). The evolutionary genetics of the family have also been intensively studied (e.g. Gill *et al.* 1989, 1993, Sheldon *et al.* 1992, Kvist *et al.* 1996, Sheldon & Gill 1996, Slikas *et al.* 1996, Ohta *et al.* 2000). We report here that the most aberrant member of the family has gone unrecognized because it has always been misclassified as a jay (Corvidae).

Hume's Ground-Jay *Pseudopodoces humilis* is a pale, cryptically coloured songbird weighing approximately 45 g, with long legs and a long decurved bill (Fig. 1). It dwells above the tree line (3300 to perhaps 5480 m) on rocky steppes and grasslands of the Tibetan (Qinghai–Xizang) Plateau (Ali 1962, Chen & Luo 1998). The birds are very active on the ground, progressing with bounding hops, while frequently stopping to flick the tail in a manner reminiscent of a wheatear (*Oenanthe*), but they fly only rarely and weakly (Schäfer 1938, Ali 1962, Chen & Luo 1998). They dig actively for insects with their strong bill in soil, turf, and yak dung.

From its initial description (Hume 1871) until 1978, *Pseudopodoces* was treated as the smallest member of the Corvidae (the crows and jays), and was usually included in *Podoces*, a genus of ground-jay with unquestioned corvine affinities. *Pseudopodoces* and *Podoces* have several traits in common: they are terrestrial

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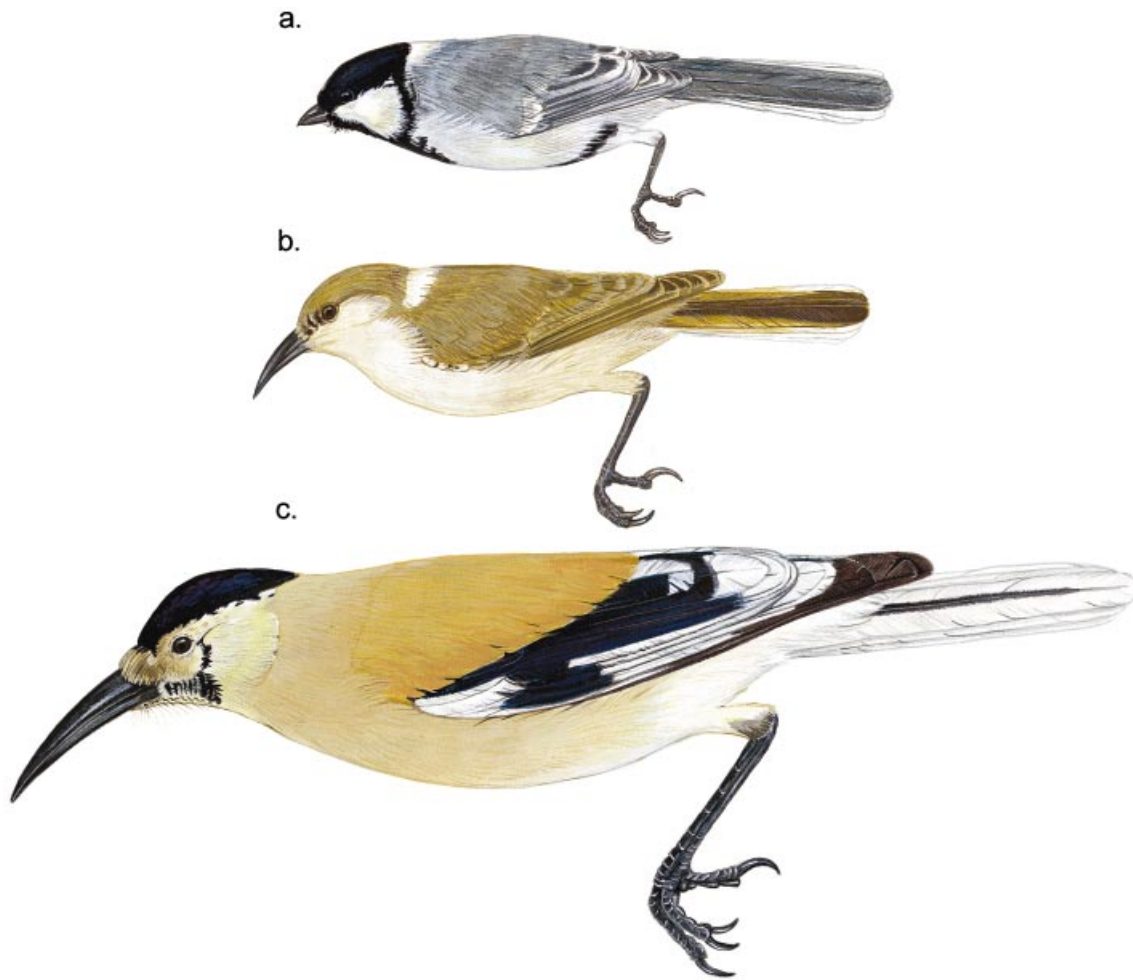


Figure 1. Comparison of skin specimens of (a) *Parus bokharensis* (Turkestan Tit), (b) *Pseudopodoces humilis* (Ground Tit, formerly Hume's Ground-Jay) and (c) *Podoces biddulphi* (Xinjiang Ground-Jay).

birds of dry, open country with pale plumage and relatively long, slender bills. *Podoces* is also an Asian genus, with four allopatric species distributed in deserts of China and the Near East. However, these four species differ markedly from *Pseudopodoces* in their much larger body size, prominent white wing patches, and patches of dark, iridescent plumage (Fig. 1). The species of *Podoces* build exposed stick nests (Goodwin 1986), whereas *Pseudopodoces* places its nest of grass and moss inside a cavity, making use of rodent burrows, crevices or tunnels that it excavates in earth banks (Ludlow 1928, Baker 1932, Schäfer 1938, Chen & Luo 1998). Both genera line the nest with wool and hair. True ground-jays of the genus *Podoces* are fleet runners (Goodwin 1986), in contrast with the exaggerated hops made by *Pseudopodoces*.

Doubts about the evolutionary relationships of *Pseudopodoces* were first raised by Borecky (1978),

based on a comparative study of appendicular muscles in the Corvidae (Borecky 1977). Because *Pseudopodoces* differed from the Corvidae in important myological characters and in having a double pneumatic fossa of the humerus, he considered its familial allocation uncertain and recommended that future studies consider a possible relationship with starlings (Sturnidae). Hope's (1989) study of the comparative osteology and phylogeny of the Corvidae led her to concur that *Pseudopodoces* should not be classified in that family. She commented that the 'distinctive upper jaw hinge [of *Pseudopodoces*] is unlike that of any corvid but resembles that of certain birds of the families Sittidae and Paridae' (Hope 1989: p. 180). Nonetheless, *Pseudopodoces* has continued to be treated as a member of the Corvidae in checklists, guides and journal articles (e.g. Monroe & Sibley 1993, Madge & Burn 1994, Cibois & Pasquet 1999).

Borecky (1978) gives a nomenclatural history of *Pseudopodoces*, which is not repeated here except to mention that Zarudny and Loudon (1902) introduced the generic name as a subgenus for *Podoces humilis*, and Stresemann (1928) later elevated it to generic rank.

METHODS

We evaluated the evolutionary relationships of *Pseudopodoces* using three independent datasets: (a) an osteological character matrix expressly designed to address the phylogenetic position of *Pseudopodoces*; (b) a nucleotide sequence dataset for the *c-myc* gene that forms part of an ongoing investigation of passerine relationships (e.g. Ericson *et al.* 2000); and (c) a nucleotide sequence dataset for the cytochrome *b* gene that is part of a larger study of relationships among the Paridae.

Phylogenetic analyses were performed with PAUP* 4.0b4 (Swofford 1998). The Wilcoxon rank-order test (Templeton 1983) was used to evaluate the hypotheses that *Pseudopodoces* is monophyletic with the Corvidae (Hume 1871), the Sturnidae (Borecky 1978), the Sittidae and the Paridae (Hope 1989). (Hope mentioned a resemblance to both the Sittidae and the Paridae.)

Osteology

Observations of traditional taxonomic characters and a preliminary survey of comparative osteology eliminated certain major groups of passerines from consideration. Nine-primaried oscines were excluded because *Pseudopodoces* has the tenth primary well developed. Thrushes (Turdidae) were eliminated because we observed that *Pseudopodoces* lacks the 'turdine thumb' of the syringeal musculature described by Ames (1975). Larks (Alaudidae) were rejected because they have a single pneumotricipital fossa of the humerus (Bock 1962), as opposed to the double fossa of *Pseudopodoces* (Borecky 1978). In the preliminary osteological survey, we found that *Pseudopodoces* differs distinctly from each of these groups but resembles the Paridae (Figs 2 and 3).

Thirty-seven species of oscine passerines were then selected for the osteological study, with the objectives of: (a) sampling the Paridae and Corvidae, (b) including taxa that other authors have proposed as relatives of *Pseudopodoces*, (c) including taxa that other authors have suggested as outgroups to the Paridae and Corvidae, (d) selecting additional taxa to

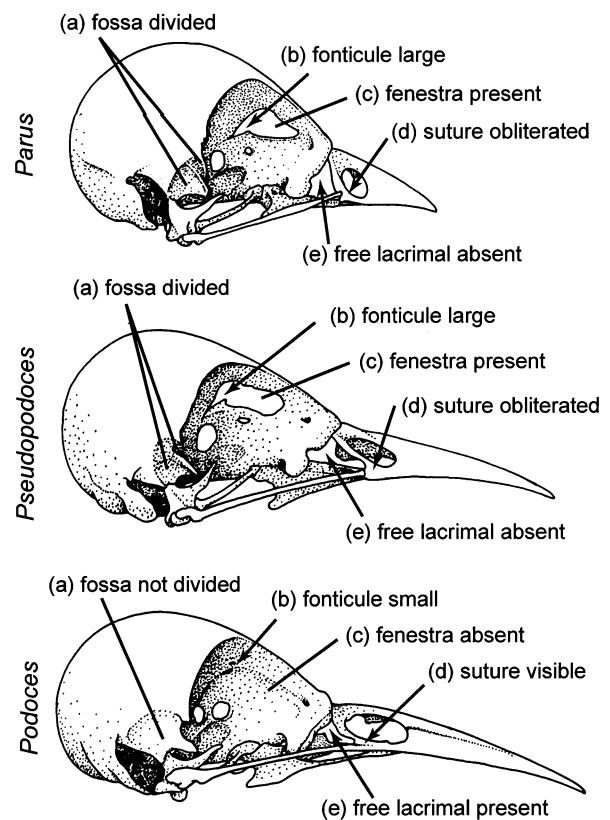


Figure 2. Lateral view of the skulls of *Parus major*, *Pseudopodoces humilis* and *Podoces hendersoni* (Mongolian Ground-Jay). Not to scale. Characters (with references to character number in appendix 1) in which *Pseudopodoces* differs from *Podoces* and agrees with *Parus* include: (a) temporal fossa partly divided by zygomatic process – 29; (b) orbitocranial fonticule large – 25; (c) dorsal interorbital fenestra present – 22; (d) nasal/premaxilla suture obliterated – 5; (e) free lacrimal absent – 20.

bridge the morphological gap between the Corvidae and Paridae, with special attention to taxa that superficially resemble *Pseudopodoces*. In the PAUP* analyses, the osteological trees were rooted on *Cormobates leucophaeus* (White-throated Treecreeper, Climacteridae), an old Australian endemic that is an apparent outgroup to all other species in the dataset (Sibley & Ahlquist 1990, Christidis *et al.* 1996).

The definition and scoring of osteological characters were based on comparisons of skeletons in the collections of the National Museum of Natural History, Washington, DC (USNM), supplemented with several skeletons borrowed from the National Museum of New Zealand, Wellington (NMNZ), and The Natural History Museum, Tring, UK (BM). The reference series of skeletons used to define the

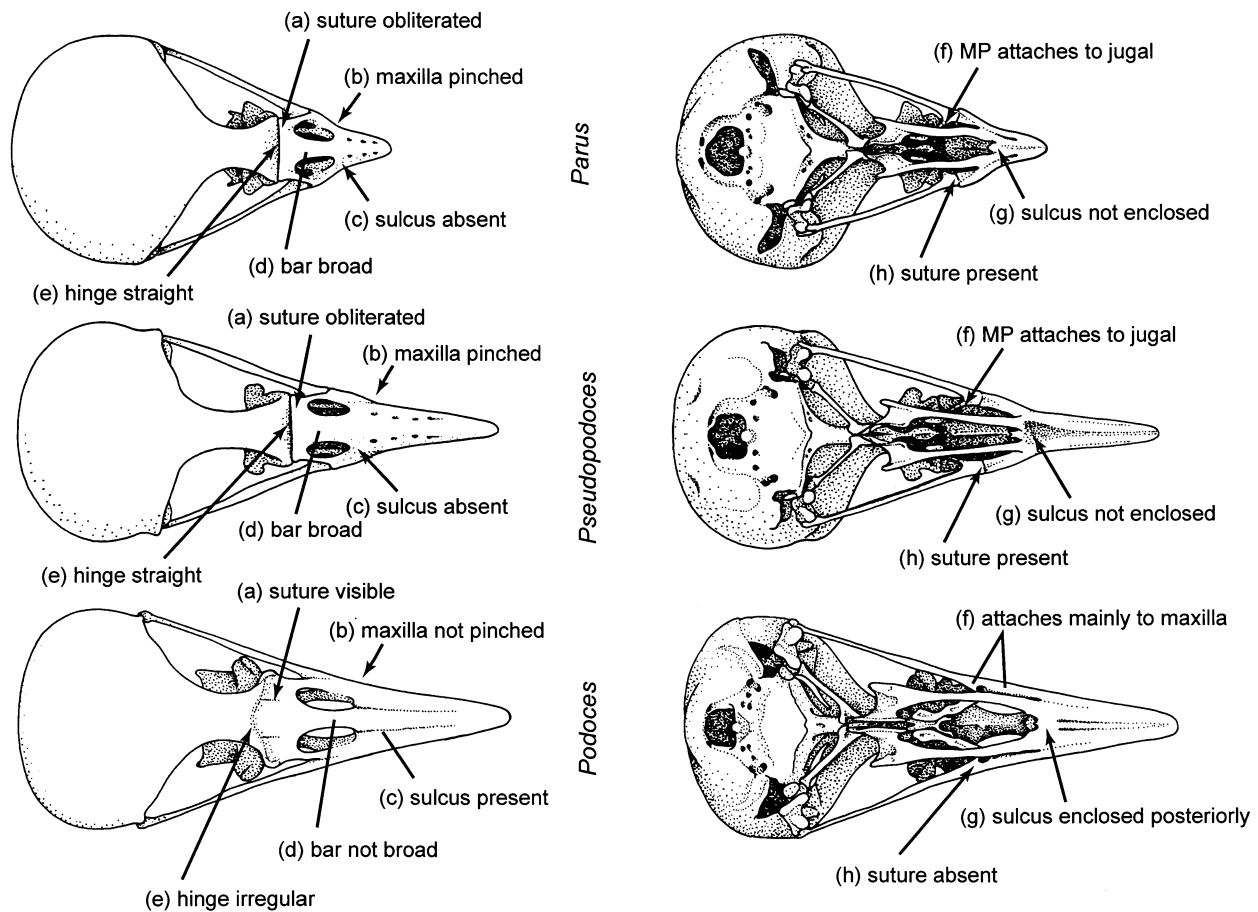


Figure 3. Dorsal and ventral views of the skulls of *Parus major*, *Pseudopodoces humilis* and *Podoces hendersoni*. Not to scale. Characters (with references to character number in appendix 1) in which *Pseudopodoces* differs from *Podoces* and agrees with *Parus* include: (a) intranasal suture obliterated in adults – 3; (b) maxilla pinched anterior to the nasals – 1; (c) absence of a neurovascular sulcus extending anterior from the nasal aperture – 4; (d) dorsal nasal bar broad – 2; (e) nasofrontal hinge straight – 19; (f) maxillopalatine (MP) attaches to jugal – 10; (g) median neurovascular sulcus not enclosed posteriorly – 9; and (h) suture present at the maxilla-quadratojugal flexion zone – 15.

characters is listed in Table 1; other specimens in the USNM collections were examined to check for variation.

Characters in which the variation could be classified into two or more discrete states were sought for inclusion in the osteological matrix. Characters were rejected if: (a) the variation could not be categorized with high repeatability across all taxa in the study; (b) polymorphism was common within terminal taxa; (c) the only variation expressed within the taxonomic sample was an autapomorphy. (Autapomorphies are uninformative in parsimony analysis.) No character was rejected on the basis of an *a priori* hypothesis that a state shared among certain taxa represented analogy rather than homology (i.e. that the state had evolved more than once). Thus,

the osteological characters represent a survey of discrete variation within the taxonomic sample, rather than a selection made with a view to minimizing homoplasy.

We found some characters in which the variation could generally be classified in two distinct states, but for which certain taxa displayed intermediate conditions. In these cases, an intermediate state was assigned, and the character was run as ordered in the PAUP* analyses. All other characters were run as unordered. The osteological matrix was analysed for parsimony, using 100 replicates of heuristic searches, with random addition of taxa followed by TBR branch swapping. As a measure of branch support, decay indices (Bremer 1988) were calculated using the program AutoDecay (Eriksson 1998). Character

Table 1. The reference series of skeletons used to define osteological characters. Specimens are complete adults except where indicated; sexes given when known.

Taxonomy	Skeletons examined	Collecting locality
Climacteridae		
<i>Cormobates leucophaeus</i> (White-throated Treecreeper)	USNM 612735 male	Australia
Meliphagidae		
<i>Anthornis melanura</i> (New Zealand Bellbird)	NMNZ 24667	New Zealand
Eopsaltriidae		
<i>Petroica macrocephala</i> (Tomtit)	NMNZ 22829	New Zealand
<i>Petroica australis</i> (New Zealand Robin)	NMNZ 19346 male, subadult	New Zealand
Corvidae		
<i>Garrulus glandarius</i> (Eurasian Jay)	USNM 491730 male	United Kingdom
	USNM 557544 female	Netherlands
	USNM 620650	India
	USNM 620649	United Kingdom
<i>Perisoreus infaustus</i> (Siberian Jay)	USNM 620133 male	Sweden
	USNM 620129 female	Sweden
<i>Podoces hendersoni</i> (Mongolian Ground-Jay)	USNM 557518 male	Mongolia
	USNM 557519 female	Mongolia
<i>Podoces panderi</i> (Turkestan Ground-Jay)	USNM 291221	unknown
<i>Pseudopodoces humilis</i> (Tibetan Ground-Jay**)	USNM 557980 male	China
	USNM 557979 male	China
	USNM 557978 male	China
<i>Nucifraga caryocatactes</i> (Spotted Nutcracker)	USNM 319585 male	China
	USNM 319586 female	China
Sturnidae		
<i>Aplonis opaca</i> (Micronesian Starling)	USNM 556237 male	Mariana Islands
	USNM 556238 female	Mariana Islands
Mimidae		
<i>Mimus gundlachi</i> (Bahama Mockingbird)	USNM 553446 male	Bahamas
	USNM 553453 female	Bahamas
Sittidae		
<i>Sitta carolinensis</i> (White-breasted Nuthatch)	USNM 553994 male	Arizona
	USNM 553996 female	Arizona
Certhiidae		
<i>Certhia familiaris</i> (Eurasian Treecreeper)	USNM 501956 male	Pennsylvania
	USNM 449515 female	Kansas
Troglodytidae		
<i>Troglodytes aedon</i> (House Wren)	USNM 487993 male	West Indies
	USNM 614142	Maryland
Poliopitilidae		
<i>Poliopitila caerulea</i> (Blue-grey Gnatcatcher)	USNM 611170 male	Maryland
	USNM 611172 female	Louisiana
	USNM 289082 female	Guatemala
Remizidae		
<i>Remiz pendulinus</i> (Eurasian Penduline Tit)	USNM 502125 female	Israel
	USNM 502223 female	Israel
<i>Anthoscopus minutus</i> (Southern Penduline Tit)	USNM 430642 female	Zimbabwe
<i>Auriparus flaviceps</i> (Verdin)	USNM 553986 male	Arizona
	USNM 571208 female	Texas
Paridae		
<i>Parus carolinensis</i> (Carolina Chickadee)	USNM 611102 male	Maryland
	USNM 611105 female	Texas
<i>Parus atricapillus</i> (Black-capped Chickadee)	USNM 502459 female	Maryland
	USNM 499696 male	Colorado
<i>Parus rubidiventris</i> (Rufous-vented Tit)	USNM 319564 male	China
<i>Parus ater</i> (Coal Tit)	USNM 500797 male	Japan
	USNM 500760 male	Japan

Table 1. Continued.

Taxonomy	Skeletons examined	Collecting locality
<i>Parus major</i> (Great Tit)	USNM 620116 male USNM 557541 female USNM 620118 male USNM 620433	Sweden Netherlands Sweden Burma (Myanmar)
<i>Parus monticolus</i> (Green-backed Tit)	USNM 611977 male USNM 318465	Taiwan Szechwan
<i>Parus caeruleus</i> (Blue Tit)	USNM 560770 female USNM 492708 male	France United Kingdom
<i>Parus inornatus</i> (Plain Titmouse)	USNM 611114 male USNM 556703 female	Colorado California
<i>Parus bicolor</i> (Tufted Titmouse)	USNM 571209 male USNM 491858 female	Texas Virginia
<i>Sylviparus modestus</i> (Yellow-browed Tit)	USNM 291764 USNM 292800 male USNM 609279 female* USNM 620563*	Szechwan Szechwan Burma (Myanmar) Burma (Myanmar)
<i>Melanochlora sultanea</i> (Sultan Tit)	BM S/1969.1.170 male USNM 620315 male*	Malaya Burma (Myanmar)
<i>Pseudopodoces humilis</i> ('Hume's Ground-Jay'*)	USNM 557980 male USNM 557979 male USNM 557978 male	China China China
Aegithalidae		
<i>Aegithalos concinnus</i> (Black-throated Tit)	USNM 431608 male	captive-zoological park
<i>Psaltriparus minimus</i> (Bushtit)	USNM 611127 female USNM 553992 male	Colorado Arizona
Regulidae		
<i>Regulus calendula</i> (Ruby-crowned Kinglet)	USNM 556758 male USNM 554729 female	California Arizona
Timaliidae		
<i>Pomatorhinus schisticeps</i> (White-browed Scimitar-Babbler)	USNM 499862 male USNM 490611 female	captive-zoological park captive-zoological park
<i>Chamaea fasciata</i> (Wrentit)	USNM 556713 male USNM 556763 female	California California
Panuridae		
<i>Panurus biarmicus</i> (Bearded Parrotbill)	USNM 621229 male USNM 621228 female	Russia Russia
Sylviidae		
<i>Sylvia nisoris</i> (Barred Warbler)	USNM 603224 male USNM 603246 female	Cyprus Cyprus

*Trunk and cranium, lacking the bill. **Here assigned to the Paridae, with the name Ground Tit.

state optimizations were examined using MacClade 4.0 (Maddison & Maddison 2000).

The *c-myc* and cytochrome *b* genes

To examine the general position of *Pseudopodoces* within the Passeriformes, 489 basepairs (163 amino acids; positions 759–1235 in chicken: Watson *et al.* 1983) of the *c-myc* gene were obtained for 25 families of oscine passerines. The nuclear *c-myc* gene evolves more slowly than mitochondrial genes, and

previous studies of higher-level taxa in birds suggest that the gene is unsaturated within passerines (Irestedt *et al.* 2001, Johansson *et al.* 2001). Two species of woodpeckers (White-barred Piculet *Picumnus cirratus* and Great Spotted Woodpecker *Dendrocopos major*) and four suboscine passerines (Yellow-bellied Elaenia *Elaenia flavogaster*, Narrow-billed Woodcreeper *Lepidocolaptes angustirostris*, Fork-tailed Flycatcher *Tyrannus savana*, and Variable Antshrike *Thamnophilus caerulescens*) served as outgroups. Methods for the extraction of DNA, PCR

amplification and sequencing followed Ericson *et al.* (2000).

The *c-myc* dataset was analysed using parsimony, with 10 replicates of random addition of taxa, followed by branch swapping. All characters were unordered. Support for individual clades was estimated by parsimony jackknifing (Farris *et al.* 1996), using Xac: Parsimony Jackknifer (Farris 1997) with 1000 replicates, each with 10 random additions of taxa and branch swapping.

In light of the osteological and *c-myc* results, the more precise relationships of *Pseudopodoces* in the context of the Paridae and Remizidae were investigated using 999 basepairs of cytochrome *b* sequence (333 amino acids; positions 15 037–16 035 in the published chicken mitochondrial genome: Desjardins & Morais 1990). The terminal taxa comprised 11 species of the genus *Parus* and three species representing three genera of remizids, with *Sturnus vulgaris* (European Starling) and *Sitta europaea* (Eurasian Nuthatch) included as outgroups.

Both parsimony and maximum-likelihood analyses were performed. The parsimony analyses were run with 10 replicates of random addition of taxa, followed by TBR branch swapping. To evaluate the effect of different mutational rates at various codon positions, three weighting schemes were employed: (a) all characters weighted equally and unordered, (b) transversions and transitions at third codon positions weighted 5 : 1 and (c) all third codon positions excluded from the analysis. For the likelihood analyses, searches used the simplest evolutionary model that yielded a significantly higher likelihood than other models. The selected model included six substitution types (Rmatrix = 0.901773, 3.11993, 0.503486, 0.0597665, 2.97589) and site-specific rates by codon position. In both parsimony and likelihood analyses, the dataset was bootstrapped (Felsenstein 1985) with 1000 and 100 replicates, respectively. The bootstrap analysis employed a simple addition sequence of taxa and TBR branch swapping.

Nucleotide sequences for the two genes were obtained from tissues in the collections of the Australian Museum, Sydney (AM), Academy of Natural Sciences of Philadelphia (ANSP), Louisiana State University Museum (LSU), Museum Victoria, Melbourne (MV), Institute of Zoology, Chinese Academy of Sciences (IZB), Swedish Museum of Natural History (NRM), University of Washington Burke Museum (UWBM) and the Zoological Museum, University of Copenhagen (ZMUC). Museum accession

numbers for the tissues and GenBank accession numbers for the nucleotide sequences are given in Table 2.

RESULTS

Osteology

Fifty-five informative characters were defined and scored (29 binary, 25 with three states, and one with four; appendices 1 and 2). Of the 25 with three states, 15 were judged to be sequential and run as ordered in the PAUP* analyses (see appendix 1). Figures 2 and 3 illustrate a selection of the cranial characters, emphasizing those that led us to consider a relationship between *Pseudopodoces* and the Paridae. Certain traits shared by *Pseudopodoces* and *Parus major* (Great Tit), such as the straight, non-overlapping articulation of the maxilla and frontal, and the obliteration of sutures on the maxilla in adults, have long been recognized as typifying the Paridae (Lucas 1890, Moreno 1985).

The heuristic searches found 72 optimal trees for the osteological dataset. *Pseudopodoces* groups with the Paridae and Remizidae on the strict consensus of these trees (Fig. 4). The basal branches that define this group are relatively robust, with decay indices of five for the branch that defines the Paridae plus Remizidae as a clade, and three for the branch that identifies *Sylviparus* (Yellow-browed Tit) as the basal taxon within it. The branch that sets the Remizidae apart as a monophyletic group also has a relatively high decay index of four. Apart from these three well-supported branches, relationships within the Paridae and Remizidae are unresolved or weakly supported.

Although character state changes on other parts of the tree also contribute to the placement of *Pseudopodoces*, the changes that occur on the basal branches for the Paridae and Remizidae are of particular interest. The unambiguous changes on the basal branch for the Paridae/Remizidae clade suggest that the following combination of traits typify these birds (character number from appendix 1 given in parentheses): maxilla distinctly pinched (1, Fig. 3), the ventral surface of the maxilla flat to convex in cross-section (8), maxillopalatine process attaches mainly to the jugal (10, Fig. 3), zygomatic process broad (26), temporal crest with a well-developed process positioned medial to the zygomatic process (27), significant bilaterally paired neurovascular foramina enter the symphyseal part of the mandible

Table 2. Tissue samples sequenced in this study, with corresponding GenBank accession numbers.

Taxonomy	Museum, tissue number	Collecting locality	GenBank number
Picidae			
<i>Dendrocopos major</i> (Great Spotted Woodpecker)	NRM 976617	Sweden	AF295164 ^{a,d}
<i>Picumnus cirratus</i> (White-barred Piculet)	NRM 976666	Paraguay	AF295174 ^{a,d}
Troglodytidae			
<i>Troglodytes troglodytes</i> (Winter Wren)	NRM 986416	Sweden	AF377272 ^a
Tyrannidae			
<i>Elaenia flavogaster</i> (Yellow-bellied Elaenia)	NRM 966970	Paraguay	AF377279 ^{a,d}
<i>Muscivora tyrannus</i> (Fork-tailed Flycatcher)	NRM 976722	Paraguay	AF295182 ^{a,d}
Thamnophilidae			
<i>Thamnophilus caerulescens</i> (Variable Antshrike)	NRM 967007	Paraguay	AF295180 ^{a,d}
Dendrocolaptidae			
<i>Lepidocolaptes angustirostris</i> (Narrow-billed Woodcreeper)	NRM 937184	Paraguay	AF295168 ^{a,d}
Corcoracidae			
<i>Corcorax melanoramphos</i> (White-winged Chough)	AM LAB1059	Australia	AY037843 ^{a,c}
Corvidae			
<i>Corvus corone cornix</i> (Carrion Crow)	NRM 986167	Sweden	AF377274 ^a
Paradisaeidae			
<i>Epimachus albertisi</i> (Black-billed Sicklebill)	MV C148	Australia	AF377278 ^a
Zosteropidae			
<i>Zosterops nigrorum</i>	ZMCU 02663	Philippines	AY037843 ^a
Oriolidae			
<i>Oriolus oriolus</i> (Eurasian Golden Oriole)	ZMCU O1376	Denmark	AF377276 ^a
Dicruridae			
<i>Dicrurus balicassius</i> (Balicassiao)	ZMCU O352	Philippines	AF377275 ^a
Turdidae			
<i>Erithacus rubecula</i> (European Robin)	NRM 976377	Sweden	AF377260 ^a
Muscicapidae			
<i>Ficedula hypoleuca</i> (European Pied Flycatcher)	NRM 976132	Sweden	AF377261 ^a
Sturnidae			
<i>Sturnus vulgaris</i> (Common Starling)	NRM 966615	Sweden	AF377264 ^a
<i>Sturnus vulgaris</i>	ANSP 3974	Pennsylvania	AF378103 ^b
Mimidae			
<i>Mimus saturninus</i> (Chalk-browed Mockingbird)	NRM 966912	Paraguay	AF377265 ^a
Sittidae			
<i>Sitta europaea</i> (Wood Nuthatch)	NRM 976163	Sweden	AF377267 ^a ,
<i>Sitta carolinensis</i> (White-breasted Nuthatch)	ANSP 4214	Pennsylvania	AF378102 ^b
Certhiidae			
<i>Certhia familiaris</i> (Eurasian Treecreeper)	NRM 976184	Sweden	AF377273 ^a
Remizidae			
<i>Remiz pendulinus</i> (Eurasian Penduline Tit)	ANSP 4381	Greece	AF347968 ^b
	NRM 966576	Sweden	AF377280 ^a
<i>Auriparus flaviceps</i> (Verdin)	LSU 19478	California	AF347969 ^b
<i>Anthoscopus minutus</i> (Southern Penduline Tit)	ANSP 5471	South Africa	AF347970 ^b
Paridae			
<i>Parus major</i> (Great Tit)	NRM 956363	Sweden	AF377263 ^a
<i>Parus major tibetanus</i>	ANSP 5454	Szechwan	AF347962 ^b
<i>Parus atricapillus atricapillus</i> (Black-capped Chickadee)	ANSP 5426	Alaska	AF347937 ^b
<i>Parus palustris palustris</i> (Marsh Tit)	ANSP 5433	Sweden	AF347943 ^b
<i>Parus montanus borealis</i> (Willow Tit)	ANSP 5436	Sweden	AF347944 ^b
<i>Parus cinctus cinctus</i> (Siberian Tit)	ANSP 5444	Siberia	AF347950 ^b
<i>Parus bicolor bicolor</i> (Tufted Titmouse)	ANSP 5450	Pennsylvania	AF347957 ^b
<i>Parus cristatus cristatus</i> (Crested Tit)	ANSP 5447	Sweden	AF347954 ^b
<i>Parus caeruleus caeruleus</i> (Blue Tit)	ANSP 5459	Greece	AF347961 ^b
<i>Parus cyanus tianschanicus</i> (Azure Tit)	UWBM CSW5839	Mongolia	AF347966 ^b
<i>Parus monticolus yunnanensis</i> (Green-backed Tit)	ANSP 5455	Szechwan	AF347963 ^b

Table 2. Continued.

Taxonomy	Museum, tissue number	Collecting locality	GenBank number
<i>Pseudopodoces humilis</i> ('Hume's Ground-Jay'*)	N 2004	China	AF377262 ^a , AF377281 ^b
Hirundinidae			
<i>Hirundo rustica</i> (Barn Swallow)	NRM 976238	Sweden	AF377270 ^a
Pycnonotidae			
<i>Chlorocichla flaviventris</i> (Yellow-bellied Bulbul)	ZMCU O1789	Kenya	AF377268 ^a
Panuridae			
<i>Panurus biarmicus</i> (Bearded Parrotbill)	NRM 966576	Sweden	AF377271 ^a
Alaudidae			
<i>Alauda arvensis</i> (Eurasian Skylark)	NRM 966614	Sweden	AF377269 ^a
Nectariniidae			
<i>Aethopyga flagrans</i> (Flaming Sunbird)	ZMCU O1346	Philippines	AF377266 ^a
Motacillidae			
<i>Anthus trivialis</i> (Tree Pipit)	NRM 976393	Sweden	AF377254 ^a
Prunellidae			
<i>Prunella modularis</i> (Hedge Accentor)	NRM 976138	Sweden	AF377259 ^a
Ploceidae			
<i>Ploceus velatus</i> (Southern Masked-Weaver)	uncatalogued	Kenya	AF377258 ^a
Icteridae			
<i>Agelaius cyanopus</i> (Unicolored Blackbird)	NRM 966916	Paraguay	AF377253 ^a
Parulidae			
<i>Geothlypis aequinoctialis</i> (Masked Yellowthroat)	NRM 956574	Paraguay	AF377256 ^a
Emberizidae			
<i>Paroaria coronata</i> (Red-Crested Cardinal)	NRM 976781	Paraguay	AF377255 ^a
Fringillidae			
<i>Loxia curvirostra</i> (Red Crossbill)	NRM 976546	Sweden	AF377257 ^a

^ac-*myc* sequences; ^bcytochrome *b* sequences; ^cthese sequences were first published by Ericson *et al.* (2002); ^dthese sequences were first published by Irestedt *et al.* (2001). *Here assigned to the Paridae, with the name Ground Tit.

in a relatively anterior position (37), the mandibular fenestra is large (38), and on the pelvis, the obturator foramen is separate from the ischiopubic fenestra (52). Additional changes for the Paridae and Remizidae exclusive of *Sylviparus* are: intranasal sutures fused and obliterated in adults (3, Fig. 3), nasal/premaxilla suture fused and obliterated in adults (5, Fig. 2), nasal cavity extends well anterior of the nasal aperture (7), a suture is present across the maxilla–quadratojugal flexion zone (15, Fig. 3), and the nasofrontal hinge is a straight, cartilaginous band (19, Fig. 3).

The unambiguous changes on the branch defining the Remizidae as a clade include possession of long and narrow transpalatine processes (18), an extensive ventral interorbital fenestra (21), long and blade-like retroarticular processes on the mandible (34), a notarium involving fusion of three or four vertebrae (41) and the absence of a fenestra or notch in the cranial cnemial crest of the tibiotarsus (54).

The c-*myc* gene

The c-*myc* dataset provides little resolution of the higher-level relationships among oscines when measured as the number of nodes receiving greater than 50% jackknife support (Fig. 5). However, the node uniting *Pseudopodoces* with *Parus* is one of the few with good support (86%). The uncorrected sequence divergence between these taxa of 1.1% is the lowest value among all pairwise comparisons with *Pseudopodoces*. Observed sequence divergences between *Pseudopodoces* and other members of the parvorder Passerida (Sibley & Ahlquist 1990) range from 1.9 to 4.8% (mean 3.16%, sd $\pm 0.90\%$, $n = 20$), while divergences with members of the parvorder Corvida range from 3.2 to 4.3% (mean 3.80%, sd $\pm 0.45\%$, $n = 5$), with suboscines from 4.6 to 5.1%, and with woodpeckers from 6.6 to 6.8%. The uncorrected sequence divergence between *Pseudopodoces* and *Corvus*, a genus of the family Corvidae, is 3.9%.

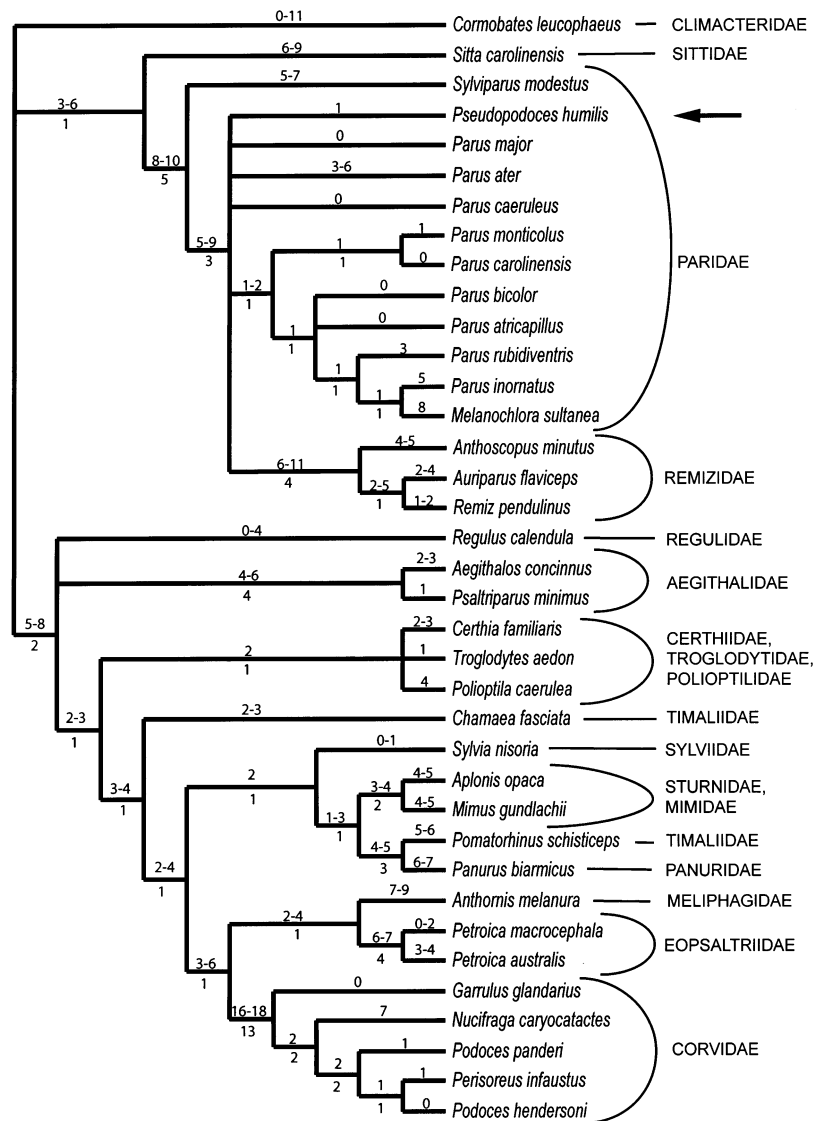


Figure 4. The strict consensus of 72 optimal parsimony trees (273 steps, CI 0.41) for the osteological dataset. Minimum and maximum branch lengths given above the branches; decay indices given below.

The exclusion of the *Pseudopodoces* from the Corvida (*sensu* Sibley & Ahlquist 1990) and inclusion in the Passerida is also supported by its possession of an insertion of three basepairs at position 789 in the *c-myc* gene (Ericson *et al.* 2000). This insertion has been demonstrated to occur in all members of Passerida investigated, but never outside this group.

The cytochrome *b* gene

In the cytochrome *b* dataset the pairwise uncorrected sequence divergences between *Pseudopodoces*

and the 11 species of *Parus* range from 8.0 to 10.9% (mean 9.3%, $sd \pm 0.80\%$). These figures are of the same magnitude as certain other pairwise sequence divergences among species of *Parus*, e.g. the highest figure is similar to that observed between *Parus cyanus* and *P. inornatus* (11.0%). The uncorrected sequence divergences between *Pseudopodoces* and the three remizid species fall between 12.6 and 16.2%, while those from *Pseudopodoces* to *Sitta* and *Sturnus* are 14.0% and 14.2%, respectively.

All analyses, including likelihood and parsimony with varied weighting schemes, produced similar

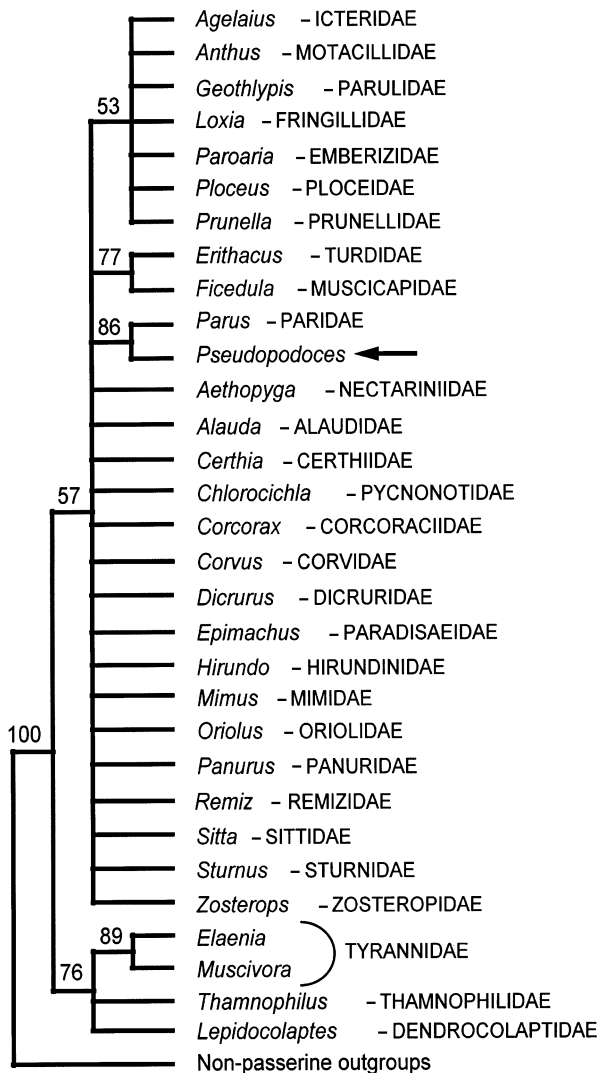


Figure 5. Parsimony tree from analysis of the nuclear *c-myc* gene (489 bp, all characters unordered). Only the branches that received support values above 50% in a parsimony jackknife analysis are shown. The 86% jackknife support for the clade with *Pseudopodoces* (arrow) and *Parus* indicates their close phylogenetic relationship.

results with *Pseudopodoces* nested within the Paridae (Fig. 6). The genus *Parus* (including *Pseudopodoces*) was recovered as a monophyletic group with high support relative to the Remizidae. The likelihood analysis provides weak support for a clade in which *Pseudopodoces* groups with *bicolor*, *inornatus*, *caeruleus* (Blue Tit), *cyanus* (Azure Tit), *major* and *monticolus* (Green-backed Tit). Within this clade, there is bootstrap support for a phylogenetic position of *Pseudopodoces* as sister to *major* and *monticolus*.

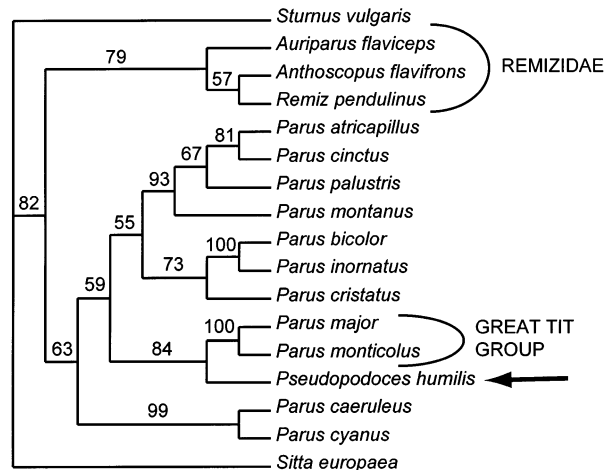


Figure 6. Maximum-likelihood tree from analysis of the cytochrome *b* data matrix (999 bp). Bootstrap percentages (100 replicates) above 50 are shown on the branches. The likelihood tree is identical in topology to the single parsimony tree from a search with transversions weighted 5x over transitions at third codon positions. The likelihood tree and parsimony trees from searches with three different weighting schemes are congruent in all nodes with greater than 50% bootstrap support.

Statistical tests

Constrained parsimony searches were used to find optimal trees consistent with the alternative hypotheses that *Pseudopodoces* is monophyletic with the Corvidae, Sturnidae or Sittidae. A one-tailed Wilcoxon rank-order test was used to determine whether these topologies are statistically worse than the optimal topologies derived from unconstrained analyses, all of which placed *Pseudopodoces* in the Paridae. For the osteological dataset, in addition to forcing *Pseudopodoces* to join the alternative clade, each constraint tree required monophyly of the Paridae and Remizidae. This step was taken to prevent the alternative clade from becoming embedded within the Paridae.

For both the osteological and the *c-myc* datasets, the constrained searches found hundreds of equally parsimonious trees. We selected one tree from each analysis for use in statistical comparisons. Rather than choosing at random, we identified a small subset of the optimal trees from each analysis that had a minimal symmetric distance from the unconstrained majority rule tree, and chose one of these. In this way, we hoped to base the statistical comparisons upon trees that were as close as possible to each other and to the unconstrained trees in topology.

The Wilcoxon tests rejected all alternative hypotheses for the relationships of *Pseudopodoces*,

except that the test on the *c-myc* dataset for a relationship with the Sittidae gave a marginally non-significant result. The significance levels, given in order for the osteological, *c-myc* and cytochrome *b* datasets, were as follows: Corvidae, $P < 0.0001$, $P < 0.02$ (not available for cytochrome *b*); Sturnidae, $P < 0.001$, $P < 0.05$, $P < 0.05$; Sittidae, $P < 0.01$, $P = 0.05$, $P < 0.05$.

DISCUSSION

Pseudopodoces exhibits little superficial resemblance to tits and chickadees, yet our results clearly indicate an underlying genetic and morphological relationship with the Paridae. The two datasets (osteology and *c-myc*) that sample a broad range of oscine taxa agree on this placement. The third dataset (cytochrome *b*) shows *Pseudopodoces* nested within the genus *Parus*. In both molecular datasets, genetic distances between *Pseudopodoces* and the genus *Parus* are smaller than between *Pseudopodoces* and other taxa. An indel (insertion/deletion) character adds further weight to the evidence that *Pseudopodoces* was misclassified in the Corvidae (Ericson *et al.* 2000).

The osteological analysis identifies the Paridae/Remizidae as a distinct osteological group within the sylvioid passerines. In osteology, *Pseudopodoces* expresses all of the character states that change on the two basal branches for the Paridae/Remizidae clade. Because the osteological data fail to resolve the reciprocal monophyly of the Paridae and Remizidae, there is an appearance of uncertainty regarding which of these two families should accommodate *Pseudopodoces* (Fig. 4). However, *Pseudopodoces* does not possess any of the osteological character states that change unambiguously on the branch identifying the Remizidae as a clade. Also, *Pseudopodoces* joins the Paridae and not the Remizidae on the *c-myc* and cytochrome *b* trees (Fig. 6). The bird's habit of nesting in cavities further supports its placement in the Paridae. All other parids are cavity nesters, whereas remizids build elaborate covered nests suspended from vegetation.

Exclusive of *Pseudopodoces*, the Paridae are a very uniform group morphologically. All possess relatively short bills. A typical parid foraging behaviour is to hold seeds or other food items underfoot while hammering them or dismantling them with the bill. This behaviour is associated with a character complex in the skull (encompassing five characters that change on the branch leading to the Paridae and

Remizidae exclusive of *Sylviparus*), including such traits as having the sutures surrounding the nasals fused and obliterated in adults, the nasofrontal hinge transformed into a straight abutment, and a suture present across the maxilla–quadratojugal flexion zone. That *Pseudopodoces* shares these traits with other parids supports an inference that it evolved from a seed-eating ancestor with a short, hammering bill. During a recent field study (Chen & Luo 1998), however, the bird was not observed to eat seeds or to hold food items underfoot and hammer on them. Stomach contents revealed a diet of insects such as caterpillars, fly pupae, adult mosquitoes and ants.

In the context of the Paridae, other unusual attributes of *Pseudopodoces* include its long decurved bill, long legs, large size, pale cryptic colouring, unspotted eggs and the lack of pneumatic openings in the pneumotricipital fossa of the humerus. Many of these attributes can be understood as adaptations to a novel adaptive zone (Bock 1979). While other tits are principally arboreal, *Pseudopodoces* dwells exclusively in high steppes and grasslands. The elongation of its legs may be an adaptation to its bounding mode of terrestrial locomotion (see Grant 1966). Loss of skeletal pneumaticity may indicate a relaxation of selection for extensive air sacs and diverticula in a bird that rarely flies. Large size may reflect physiological adaptation to high altitude. The pale coloration is reminiscent of a variety of unrelated birds that likewise inhabit dry open habitat, such as wheatears *Oenanthe* spp., hoopoes *Upupa* spp., Subdesert Mesites *Monias benschi*, Le Conte's Thrashers *Toxostoma lecontei*, roadrunners *Geococcyx* spp., Rock Wrens *Salpinctes obsoletus*, many larks (Alaudidae), and the true ground-jays *Podoces* spp. with which *Pseudopodoces* was long classified. Excluding wheatears and most larks, these birds also share long, decurved bills, suggesting that *Pseudopodoces* is just one example of a general pattern of convergence in plumage and bill shape among certain terrestrial, insectivorous birds of dry, open habitat.

Parid eggs have a white ground colour that is usually spotted with red-brown pigment (Harrap & Quinn 1996), whereas *Pseudopodoces* lays unmarked white eggs (Borecky 1978). This might suggest a relationship with *Sylviparus*, the only other parid that lays unspotted white eggs (Harrap & Quinn 1996). However, in the context of the Paridae, *Sylviparus* is primitive in lacking five cranial osteological states that appear to be functionally associated with hammering, whereas *Pseudopodoces* shares these states with typical tits. Perhaps, instead, *Pseudopodoces*

has lost the spotting on its eggs through selection or genetic drift. Gosler *et al.* (2000) recently showed that clutches within a population of *P. major* vary from unspotted to intensely spotted, and that this variation is under genetic control.

The cytochrome *b* results raise the intriguing possibility that *Pseudopodoces* is an offshoot of the Great Tit group of parid species (subgenus *Parus*) that has undergone extreme morphological evolution in a novel adaptive zone (Fig. 6). This widely distributed Eurasian subgenus occurs near the range of *Pseudopodoces* (Delacour & Vaurie 1950, Harrap & Quinn 1996). Its brightly coloured members (*P. monticolus* and the *P. major major* group of subspecies, with their green or blue-green backs and yellow underparts) could hardly appear more different in plumage from *Pseudopodoces*. However, many Asian populations in the subgenus differ less from *Pseudopodoces*, as they virtually lack bright plumage colours, being greyer above and whitish below. For example, at high elevations near the range of *Pseudopodoces*, *Parus bokharensis* (Turkestan Tit, Fig. 1) and *Parus major tibetanus* occur. Both are large, lack bright plumage and resemble *Pseudopodoces* in having extensive white in the tail.

The Great Tit species group exhibits several behavioural traits that would facilitate the invasion of treeless habitat. These birds often forage in the understorey and on the ground, and may nest at ground level (Cramp & Perrins 1993). Indeed, *P. m. tibetanus* and *P. bokharensis* often locate nest cavities in walls, earth banks or the ground (Harrap & Quinn 1996). In addition, food-caching behaviour is widespread in the Paridae but has not been reported in *Pseudopodoces*. Even this is consistent with a relationship with the subgenus *Parus*, the members of which rarely cache food (Cramp & Perrins 1993, Sheldon & Gill 1996).

Without additional supporting evidence, however, we consider the association of *Pseudopodoces* with the Great Tit species group to be tentative. In the cytochrome *b* dataset, the genetic distance between *Pseudopodoces* and *P. major tibetanus* (8.3%) is similar to distances among parid subgenera. Also, at least one myological character appears to separate the two. Borecky (1977) reports that *m. gastrocnemius pars interna* has two heads of origin plus a patellar band in *Pseudopodoces*, while Moreno and Carrascal (1993) report only one head of origin in *P. major*, a derived condition which they relate to the use of hanging postures in foraging. Moreover, the behavioural traits noted above are not exclusive to the

Great Tit group. For example, the Sombre Tit *Parus lugubris* and Azure Tit *P. cyanus* occur in treeless habitats, especially outside the breeding season, and the Coal Tit *P. ater* usually nests at ground level (Cramp & Perrins 1993).

From the cytochrome *b* results, *Pseudopodoces* could be accommodated within the genus *Parus*. Before this is done, broader taxonomic sampling within the Paridae and additional data on the comparative myology and vocalizations of *Pseudopodoces* are desired. In particular, it would be helpful to add three controversial genera of parids, *Melanochlora*, *Sylviparus* and *Cephalopyrus*, to the cytochrome *b* dataset before proposing a generic revision of the family. For now, we recommend removing *P. humilis* to the Paridae but maintaining it in the genus *Pseudopodoces*, while changing the common name to the Ground Tit.

Pseudopodoces is limited in distribution to a tectonically active geomorphological region. The high steppes that provide its habitat were created by uplift of the Tibetan Plateau due to collision of the Indian subcontinent with the Eurasian plate. This uplift is geologically recent so that the high steppes may have come into existence in the Plio-Pleistocene (Sun & Liu 2000). Our phylogenetic evidence is consistent with the hypothesis that a species of parid invaded the emergent high steppes and became the ancestor of *Pseudopodoces*. Then, morphological evolution in a novel adaptive zone so altered the species' appearance that its relationship with the Paridae was obscured, and it was long misclassified as a jay. Our new understanding of its evolutionary history creates a context for comparative studies of the behaviour, physiology and life history of this most aberrant of tits.

Maria Arvidsson, Martin Irestedt, Ulf Johansson, Mari Källersjö, Thomas J. Parsons and Tarja Rintala are greatly acknowledged for their help with obtaining the *c-myc* sequences and the cytochrome *b* sequence from *Pseudopodoces*. The osteological study was inspired by discussions with Jiri Mlíkovský, and we also benefited from the expert advice of David Danze, Ned Johnson, Pamela Rasmussen, Michael Walters and Richard Zusi. We are grateful to Taina Litwak for stipple art and Julian Hume for the acrylic painting. Mari Källersjö kindly assisted with the parsimony jackknife analyses. For the loan of specimens, we thank Mark Adams of The Natural History Museum, Tring, and Alan Tennyson of the Museum of New Zealand, Wellington. Tissue samples were kindly made available by the Zoological Museum (Copenhagen), Australian Museum (Sydney), Museum Victoria (Melbourne), Swedish Museum of Natural History, and Dr Staffan Andersson, University

of Gothenburg. Collection of tissue samples of *Pseudopodoces* was supported by the Study on the Fauna and Distribution Patterns of the Qinghai–Xizang Plateau and Adjacent Areas (KSCX2-1-06 A). Fieldwork by LFM was supported by the CAS Innovation Program.

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Received 16 October 2001;
revision accepted 11 July 2002

APPENDIX 1

Character list for the osteological matrix

Maxilla

- Dorsal view: maxilla distinctly pinched anterior to the nasals (2), somewhat pinched (1), maxilla tapers evenly anterior to the nasals (0). Ordered.
 - Dorsal nasal bar extremely broad in comparison with lateral nasal bar (1), not so broad (0).
 - Bilateral pair of sutures extending anterior from nasofrontal hinge; visible, usually open (0), obliterated or nearly obliterated (1).
 - Dorsal surface: a distinct neurovascular sulcus extends anterior from the nasal aperture to a nutrient foramen (1); the sulcus is absent (0).
 - Suture between the ventral end of the lateral nasal bar and the premaxilla: open (0); usually fused anteriorly, but open or at least visible posteriorly (1); fused and obliterated (2). Ordered.
 - Ventral margin of nasal aperture forms a dorsal crest (0); lacks a crest along at least part of its length, where it lies on the same plane as the maxillary process of the palatine (1).
 - Nasal cavity extends well anterior of the nasal aperture (1), extends slightly or not at all anterior of the aperture (0).
 - Ventral surface, exclusive of the medial neurovascular sulcus, flat to convex in cross-section (2); intermediate (1), slightly to distinctly concave (0). Ordered.
 - Ventral surface: median sulcus open (0), enclosed to form a canal posteriorly (1), enclosed to form a canal along its entire length (2). Ordered.
- Palate*
- Maxillopalatine process attaches entirely or almost entirely to the jugal arch (1); attaches to the maxilla or to both the maxilla and the jugal arch (0).
 - Maxillopalatine process distinctly pneumatized near its attachment with the maxilla and/or the jugal arch, and inflated along the ventral edge of the nasal aperture (1); not heavily pneumatized or inflated near its attachment with the maxilla and/or jugal arch (0).
 - Maxillopalatine process contacts the dorsal surface of the maxillary process of the palatine (0); contacts the lateral edge of the maxillary process of the palatine (1); free of the maxillary process of the palatine (2).
 - Strap of the maxillopalatine: narrow (0), intermediate (1), broad (2). Ordered.
 - Head of the maxillopalatine process inflated (0), flat or nearly so (1).
 - Maxilla-quadratojugal flexion zone not demarked by a visible suture between the two elements (0); the elements are separated by a visible suture, at least laterally (1).
 - Palatines: walls of partes choanalis form a long point anteriorly (0), form a short point or no point anteriorly (1).
 - Palatine: bony crest within the muscle scar for m. pterygoideus, extending anterodorsal from the transpalatine process on the medioventral face of the palatine; present (1), absent (0).
 - Transpalatine processes long and very narrow (1), relatively broad (0).

Cranium

19. The maxilla overlaps the frontal at the nasofrontal hinge, and the hinge is irregular in shape (0), the maxilla overlaps the frontal at the nasofrontal hinge, and the hinge is straight (1), the maxilla abuts the frontal at the nasofrontal hinge, and the hinge is a straight cartilagenous band (2).
20. Free lacrimal present (0), absent (1).
21. Ventral interorbital fenestra absent or set well apart from the orbital foramen (0); small to medium in size, continuous with the orbital foramen or separated from it by a narrow strap of bone (1); extensive, covering most of the length of the interorbital septum, and continuous with the orbital foramen or separated from it by a narrow strap of bone (2).
22. Dorsal interorbital fenestra present (1), absent (0).
23. Orbitocranial fonticules extend across one-half or more of the breadth of the posterior walls of the orbit (0), extend across one-third to almost one-half of the breadth (1), extend across less than one-third of the breadth (2). (View the orbital walls from the tip of the maxilla looking posteriad.) Ordered.
24. Interorbital septum partly or entirely single-walled (0), entirely double-walled (1).
25. Orbitocranial fonticules medium to large (0), small to miniscule (1).
26. Zygomatic process narrow (0), intermediate (1), broad (2). Ordered.
27. A well-developed process of the temporal crest lies medial to, and is independent of, the zygomatic process (1); the process is miniscule or absent (0).
28. A bony crest connects the postorbital process and zygomatic process (1); the crest is absent (0); the crest is so strongly developed that the two processes are essentially continuous (2). Ordered.
29. Temporal fossa not divided by the zygomatic process (0); partly divided by zygomatic process (1).
30. Foramen orbitonasale separated on the ectethmoid plate to form lateral and medial parts (0); the parts are joined in a single slit-like opening (1); the parts are joined in a single, roughly circular, opening (2).
31. Bony crest defining the temporal fossa posterodorsally: absent (0), present but gentle and rounded at its apex (1), present, well-produced, and sharp at its apex (2). Ordered.

Mandible

32. A bony crest extends from medial process to the lateral condyle, creating a flat surface of bone in the posterior view of the mandible; present (0), absent (1).
33. Lateral view: bone beneath the lateral cotyla deep posteriorly (1), shallow posteriorly (0).
34. Retroarticular process absent (0), long and blade-like (1), small and upturned (2).
35. Dorsal surface: symphyseal ridge absent (0), present (1), pronounced (2). Ordered.
36. Posterior view, lingual surface: The significant, bilaterally paired, neurovascular foramina that enter the symphyseal part of the mandible, usually near its posterior edge, are laterally placed (well separated) (0), are close-set (1), are adjacent or joined at the sagittal line (2). Ordered.
37. Dorsal view: the same neurovascular foramina enter symphyseal part of the mandible at its posterior edge (0), anterior to its posterior edge (1).
38. The mandibular fenestra is less than one-quarter the length of the pars intermedius of the ramus (0), is one-quarter to one-third the length (1), is over one-third the length (2). Ordered.

Hyoid skeleton

39. Urohyale ossified (0), unossified (1).
40. Shaft of the basihyale narrow and rod-like (0), broad (1).

Vertebral column

41. Fused thoracic and cervical vertebrae: absent (0), notarium present involving complete synostotic coalescence of the first three thoracic and sometimes the last cervical vertebrae (3), partial fusion of two thoracic vertebrae (2), spinous processes and zygapophyses of several thoracic vertebrae variably fused in some individuals (1).
42. Pneumatic openings in the cervical and thoracic vertebrae: no vertebrae with openings into the trabeculated interior of the bone (0), one or a few vertebrae with such openings (1), most vertebrae with such openings (2).
43. Bilateral recesses (perhaps to accommodate air sacs, although not opening into the trabeculated interior of the bone) present on the ventral side of the last four cervical vertebrae and sometimes the first and second thoracic vertebrae (1); recesses absent (0).
44. Paired bilateral fossae on the ventral faces of many of the synsacral vertebrae, moderately to well-developed (0), weak or absent (1).

Sternum

45. Pneumatic foramina on the dorsal surface: absent (0); extensive, especially across the cranial one-third of the bone and along the mid-line (1); a single opening (sometimes several) near the rostrum (2).

Coracoid and furcula

46. Pneumatic openings present on both the acrocoracoid process of the coracoid and the adjacent epicleidium (*extremitas omalis*) of the furcula (2); present on the acrocoracoid process only (1); absent from both bones (0).
47. Cranial process on the medial edge of the sternal end; moderately to well developed (0), small or absent (1).

Humerus

48. Pneumotricipital fossa single (0), double (1).
49. Pneumotricipital fossa non-pneumatic (or variably with a single tiny opening) (0); pneumatic, with bony trabeculae near the major opening(s) (1); pneumatic, having a single large opening with no trabeculae near its aperture (2).

Ulna

50. Olecranon process slender (0), intermediate (1), stout (2). Ordered.

Pelvis

51. Pelvis-synsacrum suture obliterated near the caudal end (1), visible near the caudal end (0).
52. Obturator foramen open to the ischiopubic fenestra (0), separated from the ischiopubic fenestra by a bony bridge between the ischium and pubis (1).

Tibiotarsus

53. Proximal end: bony ridge separating the incisura tibialis and fossa retropatellaris; absent (0), present but not produced (1), produced (2). Ordered.
54. Small fenestra in the cranial cnemial crest; absent (0), present but not completely enclosed (1), present and completely enclosed (2). Ordered.

Tarsometatarsus

55. Lateral plantar crest does not extend toward or contact the hypotarsus (0), extends toward and sometimes contacts the hypotarsus (1), fuses to the hypotarsus (2).

