A new cockatoo (Psittaciformes: Cacatuidae) from the Tertiary of Riversleigh, northwestern Queensland, and an evaluation of rostral characters in the systematics of parrots

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The first Tertiary cockatoo or any psittaciform from Australia is recorded from an incomplete rostrum from the Riversleigh deposits of northwestern Queensland, Australia. It is placed in the extant genus Cacatua but cannot be diagnosed at the specific level. This cockatoo was probably similar in size to the modern C. roseicapilla, with a short, unspecialized crest and probably white plumage. The rostrum is useful in studies of the systematics of parrots. Rostral characters support some traditional subdivisions of the order, while suggesting that others warrant re-examination.

Parrots comprise one of the most distinctive orders of birds. The approximately 340 living species of Psittaciformes have a pan-tropical and southern distribution. Of these birds, the cockatoos (Cacatuidae), with 18–21 species in five genera, centred on the Australo–Papuan region, form one of the most characteristic groups. With five genera and 10–12 species, Australia is the centre of cockatoo diversity, although species extend as far as the Philippines in the north, Sulawesi and the Sunda Islands in the west and the Solomon Islands in the east (Forshaw 1981). These birds form one of the most distinctive elements of the Australian avifauna. Despite this wide distribution, there is only a very limited fossil history of parrots (Olson 1985). At present the known record contains only a handful of Tertiary taxa, none of which is a cockatoo. From Australia, with 55 extant species, no pre-Pleistocene material has been reported (Vickers-Rich 1991). The only cockatoos are of Pleistocene age and can be assigned to extant species (Baird 1985, 1991).

Described here is a fossil cockatoo from the Early to Middle Miocene of northwestern Queensland, constituting the oldest fossil record of the order for Australia and of the Cacatuidae for the world.

FOSSIL HISTORY
The fossil record of the Psittaciformes has been summarized by Olson (1985). The earliest report is Palaeopsittacus georgei Harrison (1982) from the Lower Eocene of England, although there have been doubts expressed about the identification (Olson 1985). Mourer-Chauvire (1982) noted remains from the Upper Eocene of France, which she assigned to the Psittacidae without elaboration.

Only two Miocene records have so far been published, although P. Ballman (pers. comm. to Olson 1985) has drawn attention to the recovery of some as yet undescribed parrot remains from the Middle Miocene of Germany and France. Milne-Edwards (1867–1871) described Psittacus verruca from the Early Miocene of France, for which Lambrecht (1933) later proposed the new generic name Archaeopsittacus. Watmore (1926) named Conuropsis fratercula, the only pre-Pleistocene record of this order from the New World. No bills or skulls of these Tertiary forms have thus been reported, and it is not possible to determine at what stage these early parrots were in the evolution of the distinctive cranial morphology that characterizes parrots.

All previous Australian records of the Psittaciformes are of Quaternary age and are indistinguishable at specific level from Recent taxa (Baird 1991). Smaller, non-cacatuine forms have been reported from several sites (e.g. Hope et al. 1977, Rich et al. 1983, Baird 1985; summarized in Baird 1991); other psittacine material has not yet been evaluated. Cockatoos have only recently been reported from the fossil record—none was listed by Brodkorb (1971)—and these have been only from southeastern Australian sites. The identified species are all referable to living taxa: Red-tailed Cockatoo Calyptorhynchus magnificus, Glossy Cockatoo C. lathami, Black Cockatoo C. funereus, Gang-gang Callocephalon fimbriatum, Long-billed Corella Cacatua temnuiostra and Galah C. roseicapilla. Other cockatoo material, as yet unpublished, has been recovered from a number of other Pleistocene sites (R.F. Baird, pers. comm.).

GEOGRAPHIC AND GEOLOGIC SETTING
The Riversleigh deposits are located on Riversleigh Station, approximately 200 km north of Mount Isa, northwestern Queensland. More than 100 sites and local faunas are now known from this area but few of these have been described in the literature. Preliminary stratigraphic relationships have been determined by Archer et al. (1989), but these, as well as the interpreted ages, must be regarded as tentative.

The fossil subject of this paper came from the RSO Local
Fauna from RSO Site. This site is at the lower end (180 m a.s.l.) of the Godthelp Hill Sequence, which forms part of System B of Archer et al. (1989). System B, a collection of regionally clustered sites differing in age but not significantly in position and/or spatially isolated but approximately contemporaneous, is considered to be Early to Middle Miocene. It appears to represent fossil assemblages accumulated in pools or shallow lakes (Archer et al. 1989).

Based primarily on information derived from the rich and diverse mammal remains, Archer et al. (1989) have interpreted the vegetation of Riversleigh at this time to have been "dense, species-rich gallery rainforests probably similar to those that persist today in mid-montane New Guinea."

MATERIALS AND METHODS

Measurements were made with vernier calipers accurate to 0.05 mm and rounded to the nearest 0.1 mm.

Names of psittaciform taxa follow Forshaw (1981) except for changes based on more recent studies. For convenience of reference, three families of Psittaciformes are recognized in the discussion of this fossil (after Forshaw 1981): Loridea (lorikeets and lories), Cacatuidae (cockatoos) and Psittacidae (all other parrots).

The fossil material referred to herein is currently held in the collections of the Vertebrate Palaeontology Laboratory, University of New South Wales but will be transferred to the Queensland Museum at the completion of this study; prefixes to registration numbers for these institutions are AR and QM, respectively.

ANALYSIS OF CHARACTERS

The decurved upper mandible of parrots is distinctive, constituting one of the major external characters by which these birds are recognized. A few other orders of raptorial birds have superficially similar hooked bills, but each group can be easily distinguished from parrots by a combination of characters, not all applicable to each group, e.g., presence and shape of the naso-frontal hinge, shape of the nostrils, presence of a nasal tubercule, absence of a bifurcated groove on the upper surface that runs from the cere region towards the tip. The presence of this groove is diagnostic for the Psittaciformes.

The most easily recognized feature of parrot bills is the groove on the upper surface that runs from the cere region down the internarial septum and then bifurcates, continuing along each side of the culmen towards the tip. The presence of this groove is diagnostic for the Psittaciformes.

There are about 340 species of living or recently extinct species of parrot placed in 81 genera (Forshaw 1981). In order to assess the relationship of the fossil rostrum, 10 characters were evaluated from skulls. The characters and the states used are given in Appendix I and illustrated in Figure 1. There is a degree of arbitrariness to the scoring of some characters. Some taxa do not fit comfortably into the categories adopted, but some limitation has been made on the number of categories used to accommodate unique examples. The rhamphotheca often bears little resemblance to the underlying bone and, together with the cere, prevents any external assessment of the rostral characters. The taxa examined are listed in Appendix II. Rostral characters for many Australo-Papuan and selected extralimital psittaciform genera are given in Appendix III. These should be useful in the identification of unknown rostra.

SYSTEMATIC PALAEONTOLOGY

The Riversleigh rostrum clearly belongs to the Cacatuidae. A suite of character states serves to identify any member of this family. Most of the character states are found in other taxa; however, the shape of the naso-frontal hinge and the specialized configuration of the cere region are diagnostic.

Five genera of cockatoos are currently recognized: Probosciger (Palm Cockatoo, 1 species), Calyptorhynchus (black cockatoos, 3–5 species), Callocephalon (Gang-gang, 1 species), Cacatua (white cockatoos, 12–13 species) and Nymphicus (Cockatiel, 1 species). The character states, particularly of the nostrils, and the shape and size of the rostrum, indicate that the fossil parrot from Riversleigh is most similar to, and indeed inseparable from, Cacatua.

The other cacatuine genera can be distinguished from Cacatua by the following rostral characters:

Callocephalon. Cere region saddle-shaped with thin centre; nostrils oriented to the side (30° from midline of culmen); length : width ratio smaller than in all cacatuid species except for some individuals of C. sulphurea.

Calyptorhynchus. Cere region saddle-shaped with thin centre; internarial septum wider; nares small, directed to side; size large (compared with small Cacatua species).

Probosciger. Internarial septum wider; nares small, directed to side; size very large; shape diagnostic.

Nymphicus. Cere region spade-shaped (Fig. 1B); internarial septum narrow; size small.

Order PSITTACIFORMES Wagler, 1830
Family CACATUIDAE

(Rostrum) Naso-frontal outline with centre raised and rounded, extending above point of attachment with skull; cere region smoothed and raised as saddle-shaped platform (shape different in one species); corners of naso-frontal hinge extended into acutely angled horns (approximately 90° in one species); internarial septum medium to very wide (narrow in one species); nares small to large, facing directly forward or towards the side; tomium sigmoid shaped; size medium or large (one species small, one very large).
Figure 1. Characters and character states used in identifying rostra of parrots (see Appendix I for detailed descriptions).
A NEW COCKATOO FROM QUEENSLAND

MEASUREMENTS
Culmen length (tip broken) 20.6 mm; width of naso-frontal hinge from caudolateral corner to midpoint 9.3 mm; greatest dorsoventral distance 17.2 mm; greatest rostrocaudal distance 15.1 mm; width of internarial septum at midpoint 5.4 mm.

DESCRIPTION
Rostrum with damage to the right side, caudal end, tip, and some areas on the left side above and below the left orbit, along the tomium and caudoventral corner. In anterior view, lateral side slightly concave; top margin extending laterally then curving medially at about 60° forming a distinct acute 'horn'; cere region raised and flattened, distal side concave, other sides not discernible owing to damage; nostrils medium, forward facing, set on side of rostrum about equidistant between culmen and cranial border; internarial septum wide; groove along midline of culmen, curving right just distal of line connecting midpoints of nares, at which point another groove curves left, both continuing along the respective sides of the culmen towards the tip. In lateral view, tomium deep at posterior, curving concavely dorsad below nostril, then ventrad towards tip; caudalmost section of tomium lost through abrasion. In ventral view, premaxilla concave with a narrow slit-like opening along caudal end of rostrocaudal midline; maxilla more dorsal, rostral end undercutting caudal end of premaxilla, slightly concave, thin ridge running along rostrocaudal midline with a slit-like opening on either side of rostral end. In caudal view, many surfaces abraded, no obvious features present.

Based on size and form, the Riversleigh bird cannot be distinguished from some similarly sized extant species, such as roseicapilla and smaller individuals of pastinator. Thus, it is not possible to assign a specific name to this taxon at present.

Cacatua species indeterminate

DISCUSSION
Two major subdivisions can be recognized within Cacatua (Adams et al. 1984). One group is characterized by the possession of heavy bills, upcurving coloured crests and round wings (alba, galerita, leadbeateri, moluccensis, ophthalmica, sulphurea); within this group leadbeateri and alba have substantially smaller bills than the other species but are alike in the shapes of the crests and wings. The other subdivision has smaller bills, short uncoloured crests and more slender wings (ducorpsi, goffini, haematuroptila, pastinator, roseicapilla, ten uirostris). Large individuals of the larger species (e.g. pastina-
ator) approach and possibly slightly overlap smaller examples of leadbeateri and alba in bill size.

On the basis of bill size, the Riversleigh bird most likely belongs to the small-billed group of white cockatoos. It is smaller than the smallest individuals of the large-billed group. Assuming that the correlation of the other characters holds, this form would have been a relatively small cockatoo with a short, unspecialized, uniformly coloured crest. Following this trend of modern species, its plumage would have been predominantly white.

Although the tip is missing, it is almost certain that the bill of the Riversleigh bird was not elongated as in C. tenuirostris. Given the small basal cross-section of the broken tip, the tip, if attenuated, would have to have been so to a degree in excess of any living form. The inward curvature of the distal end eliminates this as a possibility.

Although it is possible to determine to which section of the genus the Riversleigh bird probably belongs, the fossil gives little information about the phylogenetic history of the genus. Its morphology is as modern as any extant member of the species, indicating that the genus was present in an essentially modern form by the early Miocene. There is nothing to rule out that large-billed species were not also contemporaneous.

Both groups have representatives on the Australian mainland (large-billed: galerita, leadbeateri; small-billed: pastinator, tenuirostris, roseicapilla). The large-billed species are centred on New Guinea (galerita), with species occurring on the islands directly to the west (moluccensis—southern Moluccas; sulphurea—Sulawesi, Sunda Islands) and east (ophthalmica—Bismarck Archipelago). Small-billed forms are mosaically distributed among these to the south (Tanimbar Islands—goffin) and west (central and northern Moluccas—alba) of New Guinea, and on the periphery of the genus's range to the north (Philippines—haematropygia) and east (Solomon Islands—ducorspi). Other than on the Australian mainland, no more than a single species occurs at any locality.

As an environmental indicator, the Riversleigh bird neither corroborates nor contradicts current ideas on the climate and vegetation at Riversleigh during the Early to Middle Miocene. In Australia, the smaller members of Cacatua (roseicapilla, tenuirostris, pastinator) are birds of the open meadow, semi-arid and arid zones. On the periphery of the range of the genus, ducorspi, goffin and haematropygia occur in both primary rainforest and secondary growth, also entering agricultural areas for crops (Forshaw 1981). Therefore, while the presence of the Riversleigh bird is consistent with a rainforest environment, it is not contra-indicative of drier, more open habitats.

SYSTEMATIC USE OF THE ROSTRUM IN THE PSITTACIFORMES

Parrots are an intensively studied group, with a wide range of morphological, anatomical, pterylographic and behavioural characters having been used by numerous authors (for a summary of previous work and characters, see Smith 1975). Despite this attention, parrot systematics are far from settled.

Although previously ignored, the rostrum of parrots has some value in the systematic study of this group. Features of the external bill have been used in systematic studies but have almost invariably referred to aspects of the external rhamphothecal covering, not to the underlying bone. The correlation between the external features and their appearance on the bone is not high, and, indeed, some of the characteristic bill morphologies that are apparent when the rhamphotheca is present are reduced to considerable uniformity in its absence. Some characters of the rostrum appear more related to peculiarities of feeding and food choice than as clues to a taxon's phylogenetic background. Thus rostrum shape, length: width ratio and size may be important in diagnosing certain taxa but have only limited use in suggesting relationships with other psittacine groups. Some other character states are at least somewhat related to overall bill size. On the other hand, several characters are particularly valuable in indicating where relationships lie. In various combinations, the nasa-frontal hinge outline and corners, cere region configurations, internarial septum width, tomium shape, nostril size and orientation, and culmen curvature can aid in the diagnosis of various subgroups of the parrots.

This survey was not intended to be a thorough systematic study of the rostra across all taxa in the Psittaciformes. Additionally, there are other characters that could be scored in a more detailed study, such as bill curvature perpendicular...
ular to the culmen, the configuration of the narial region, shape of the tip, etc. Nonetheless, the limited examination of the rostra performed here allows some comments to be made on aspects of parrot systematics. Even where no useful indication of relationships is obtained, the scores of each taxon should assist in the identification of unknown taxa.

The cockatoos are easily the most distinctive group of parrots on the basis of rostral morphology. These characteristic features were discussed above. Several subgroups can be recognized: Probosciger is distinctive, but its oversized rostrum is so extensively modified that many of its characteristic features were discussed above; Callocephalon and Calyptorhynchus are similar in having similar cere region configurations and lateral orientations of the nares; Cacatua is set apart by the cere region configuration and the size and orientation of the nostrils.

The Cockatiel Nymphicus hollandicus has had a chequered taxonomic history; some authors placed it with the Polytelinae or Platycercinae (Verheyen 1956, Brereton 1963, Condon 1975) and others assigned it to the Cacatuidae, usually as a sister taxon to the other genera of cockatoos (Salvadori 1891, Thompson 1900, Reichenow 1913, Peters 1937, Glenny 1957, Holyoak 1972, Smith 1975, Wolters 1975–1982, Forshaw 1981, Adams et al. 1984). The rostrum demonstrates unequivocally that Nymphicus is a cockatoo. It has the features of the raised cere region configuration that characterizes this group. Its unique form of the raised cere region indicates that it is separate from the other cockatoos at a significant level.

Another major section of the Psittaciformes is the lorikeets and lories, Loridiidae. While not as easily diagnosed on rostral characters as the cockatoos, this group can nevertheless be segregated on a suite of character states. These include the cranially flattened culmen, relatively straight tomium, rounded naso-frontal outline and correlated obtuse corner angles and the very thin interfrontal septum.

Three of these groups can be identified on the basis of rostral shape, but there are few other clues to where their relationships lie. The fig parrots (Opopsis, Psittacus, and Polytelinae) have noticeably broad rostra, the width approaching the length more closely than for any other similarly sized forms.

Other than their very different rostral shapes, Nestor and Strigops are superficially similar. The character states by which they resemble one another are also widely distributed in other genera and appear generalized; therefore, they may have little significance. The more defined cere region appears to characterize many larger forms that are otherwise not closely related.

Most of the features of the platycercine rostrum seem unspecialized and undiagnostic. Only the curvature of the culmen, with its flattened cranial end and projection on the septum, serves to identify the component taxa of this Australasian group. Lathamus has long been problematic to parrot systematists. On the basis of its tongue modified for nectar feeding, some authors (Peters 1937, Wolters 1975–1982) have associated it with the lorikeets. Forbes (1879) considered it allied with the fig-parrots. Verheyen (1956) and Glenny (1957) created a separate subfamily for it. Generally, it has been agreed that, despite some superficial similarities to other groups, Lathamus belongs with the platycercines. Examination of the rostrum supports this conclusion. Not only does it have the characteristic culmen curvature and projection of the platycercines, it has a wider internarial septum and tomium shape than do the lorikeets.

The remaining Old World taxa are often separated into two subgroups: the large African forms (Psittacus, Coracopsis and Poicephalus; Psittacinae) and the primarily Asian, Australo–Papuan and South Pacific forms (Agapornis, Geoffreyus, Eclectus, Psittacula, Tanynathus, Polytelis, Aprosmictus and Prosopeia; Psittaciformes). The latter is sometimes divided, segregating the last four Australo–Papuan and South Pacific genera in the Polytelinae.

Divisions within these Old World forms can be discerned but show some inconsistency with the traditional boundaries. Agapornis, Psittacula and Poicephalus are the only genera surveyed that have large, upwards directed nostrils; the nostrils of Tanynathus are also directed upwards but are proportionally smaller (probably a consequence of the oversize bill.) Eclectus stands apart on a combination of septum width, size of the nares and the unique configuration of the cere region. The other genera do not differ substantially from each other, and all appear relatively generalized in their character states, based on distribution of these features through the parrots.

Peters (1937), Glenny (1957), Smith (1975) and others have included the New World taxa in a single tribe/subfamily without further internal division, whereas Salvadori (1891), Thompson (1900), Reichenow (1913), Verheyen (1956), Brereton (1963) and Wolters (1975–1982) distributed these among at least two subgroups (although with differing combinations of component taxa). There is an indication that there are indeed several diagnosable subgroups.

Although there are differences between them, Anodorhynchus, Ara, Aratinga, Conuropsis, Cyanoliseus, Enicognathus, Myiopitta, Pionites, Pyrrhura and Rhynchopsitta all share some character states with restricted distribution: nostrils that are small (markedly so in Myiopitta) and directed upwards or sideways. Ara manilata differs from all other examined taxa of this assemblage, including other members of its genus, in both characters. (Anodorhynchus and, to a lesser extent, Ara approach Probosciger in some characters. This plasmonic expression seems directly related to their disproportionate large size.) All these genera are frequently segregated in the Conurinae. Brotoegeris is usually also included here but it differs in its larger, forward-facing nostrils.

The other New World genera examined, Amazona, Pionus, Touit, Forpus and Bolborhynchus, share the widespread and apparently generalized large, forward-facing nares. They are sometimes placed in the same subfamily, sometimes in separate ones (the first three in Amazoninae, the last two in Forpiniae). None has obviously unusual features, although they do differ from each other in several states. Without additional representatives of each assemblage, it is not pos-
sible to assess the importance of this variation. On the basis of purported similarities with the platycercines, Breteron (1963) placed the Forpidae in a different superfamly from the other New World genera, near the Platycercidae. Forpus and Bolborhynchus both lack the platycercine culmen projection but otherwise agree with the Australian group in its generalized characters.

This cursory survey of rostral characters was initially undertaken to make possible the identification of isolated parrot rostra, and it has been shown that, for some groups of these birds, identification can be made even to species level. It was also revealed that the rostrum provides useful information towards the systematic study of the Psittaciformes. Some traditional groupings are strongly supported. Some others are brought into question and deserve further examination. Rostral characters should not by themselves be the basis for classifying parrots, but they can serve as valuable adjuncts to other character systems in broad-based systematic work on these birds.

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REFERENCES


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APPENDIX I

Characters and character states used in identifying rostra of parrots

See Figures 1A–J for illustrations of each character state.

(A) Outline of naso-frontal hinge (Fig. 1A)

The shape of the naso-frontal hinge when viewed from directly in front.

1 Slightly but smoothly rounded convexly over entire length with no indentation at the midpoint (e.g. Trichoglossus);
2 Slightly indented at the centre, the remainder of the hinge being more or less straight (e.g. most Psittacidae); slightly elevated through the centre region (e.g. Lorius, Agapornis, Eclectus, Nestor) or slightly convexly rounded (e.g. Melopsittacus, Psittacillostris);
3 Slightly to moderately elevated through the centre region with a gradual angle at the commencement of the rise and without any indentation (e.g. Amazona, Psittacus);
4 Considerably elevated through the centre region with a marked angle at the commencement of the rise and no indentation (e.g. most Cacatuidae); a variation on the last condition is seen in Probosciger, which has the centre region markedly swollen obscuring a definite sharp angle at the commencement of the rise. In lateral view, in the first three conditions the highest level of the naso-frontal hinge is even with or just lower than or slightly above the point of attachment with the skull; in the last the raised centre extends above this point, sometimes markedly so.

(B) Configuration of cere region (Fig. 1B)

Somewhat correlated with the previous character is the configuration of the area circumscribed by the rear edge of the nares, the (usually) proximal end of the internarial septum and the naso-frontal hinge—the region covered by the fleshy cere.

1 Extending across the base of the rostrum and depressed below the level of the hinge and the remaining of the rostrum (only observed in Eclectus among taxa examined);
2 At the same level as the naso-frontal hinge and either (a) with a slight indentation in the centre (e.g. Polytelis, Barnardiis, Platycercus) or (b) without an indentation and more or less level or even slightly rounded (e.g. Pezoporus, Lorius, Strigops); some taxa, particularly larger forms and platycercines, exhibit a more clearly defined distal border to this area (*) (e.g. Nestor, Strigops, Platycercus);
3 Most or part of the region raised in a discrete area: (a) saddle-shaped broadly across entire base of septum, distal border concave, wide in lateral profile (Cacatua); (b) saddle-shaped but very thin across base of septum, widely concave distally, narrow in lateral profile (Calocephalon, Calyptorhynchus); (c) across entire central cere region, distal border straight and extending further distally along internarial septum, wider in lateral profile than Cacatua (Nymphicus);
4 Raised in non-discrete area, very bulbous, no distinct borders but with faint indication that it resembles condition 3a, very wide lateral profile (Probosciger).

(C) Lateral angle of naso-frontal hinge (Fig. 1C)

The angle formed by the junction of the naso-frontal hinge and the lateral margin of the rostrum and the configuration of this corner region.

1 End of naso-frontal hinge rounded, lateral margin vertical, forming obtuse angle, c. 120° (e.g. Trichoglossus, Glossopsitta);
2 End of naso-frontal hinge more or less straight, lateral margin vertical, forming approximately 90° angle (e.g. Alisterus, Cyanoramphus);
3 End of naso-frontal hinge more or less straight, lateral margin angled slightly towards midline of rostrum, forming a slightly acute angle, c. 60–75° (e.g. Eclectus, Platycercus, Psittacus);
4 End of naso-frontal hinge more or less straight, lateral margin slightly acute at junction then becoming more vertical, forming small but nonprominent ‘horn’ at corner (e.g. Prosopeia, Strigops);
5 End of naso-frontal hinge more or less straight, lateral margin sharply acute at junction then becoming more vertical, forming large and prominent ‘horn’ at corner (e.g. Cacatua, Calocephalon, Calyptorhynchus, Nymphicus).

(D) Width of internarial septum (Fig. 1D)

This is a somewhat subjective combination of the overall width of the septum and its size in relation to the entire upper mandible. The width of the septum is the length of the arc taken from one side of the tomium across the dorsal surface, passing through this midpoint and continuing to the other side.

1 Very thin. Septum ≤ 1 mm or between 5% and 10% of the rostrum arc length (e.g. Trichoglossus, Glossopsitta, Psophotus);
2 Thin. Septum 1–2 mm or about 10% of the rostrum arc length (e.g. Nymphicus, Barnardiis, Polytelis);
3 Medium. Septum about 3–5 mm or between 10% and 20% of the rostrum arc length (e.g. Amazona, Prosopeia, Strigops);
4 Medium wide. Septum about 7 mm or about 25% of the rostrum arc length (septum width about the same as that of lateral section of rostrum between the nares and tomium) (Cacatua, Eclectus);
5 Wide. Septum >10 mm or >30% of the rostrum arc (septum width greater than that of lateral section of rostrum between the nares and tomium) (Probosciger, Calyptorhynchus, Calocephalon, Cacatua sulphurea).

(E) Size of nares (Fig. 1E)

Two measures of nostril size have been made: one is based on the opening viewed facing them from their direction of orientation, the other is the extent of the opening along the side of the nostril in lateral and dorsal views. Both assessments are somewhat subjective,
based in part on the absolute size and the proportional size relative to the rest of the rostrum. Narial width is that across the diameter of one naris; the proportional width is based on both nostrils and is measured in a manner similar to proportional septum width. In forward aspect the states are:

1. **Small.** One naris <3 mm or both constitute less than 20% of rostrum arc length, narial diameter is less than the width of the septum and of the lateral edge between the naris and tomium (Myiopsitta, Calyptorhynchus latami);

2. **Medium.** One naris 5-6 mm or both constitute between 20% and 35% of rostrum arc length, narial diameter is always less than the width of the septum and usually less than that of the lateral edge between the naris and tomium (e.g., Eclectus, Probosciger, Calyptorhynchus, Callocephalon);

3. **Large.** One naris >6 mm or both constitute more than 35% of rostrum arc length, narial diameter is greater than or equal to the width of the septum and of the lateral edge between the naris and tomium (e.g., most psittaciforms examined).

The size of the nares in lateral and dorsal aspect seems to some extent to be related to the overall size of the rostrum, with the larger species exhibiting the greater lateral/dorsal extent; this does not hold for the Cacatuidae. This character is not as easily scored as the width in forward aspect. The states for lateral/dorsal extent are:

**Small.** More or less equal (1 x) to the width in forward aspect, in lateral view round naris in shape (e.g., Cacatua, Callocephalon, Nympheus, Eclectus, Platycercus, Myiopsitta);

**Moderate.** Between 1 x and 1.5 x the width in forward aspect, in lateral view nares somewhat oval in shape (e.g., Trichoglossus, Alisterus, Prosopeia, Barnardius);

**Marked.** Between 1.5 x and 2 x the width in forward aspect, in lateral view naris oval and elongated in shape (Nestor, Strigops, Amazona).

(F) **Orientation of nares (Fig. 1F)**

The angle of orientation is judged relative to the horizontal and to a vertical plane passing through the distocranial midline. Within the general categories, several substates are discernable.

1. **Forward.** Nares oriented laterally less than 10° from forward and less than 10° above vertical (most psittaciforms examined);

2. **Sideways.** Nares oriented laterally more than 30° from forward and less than 60° above vertical: (a) 0° above horizontal, 45-60° to side (Probosciger); (b) 30° above horizontal, 45° to side (Calyptorhynchus);

3. **Upward.** Nares oriented laterally less than 30° from forward and more than 60° above vertical: (a) 75° above horizontal, 30° to side (e.g., Agapornis); (b) greater than 75° above horizontal, 15-20° to side (Myiopsitta).

(G) **Distocranial curvature (Fig. 1G)**

In lateral view, the curve of the culmen may be smoothly rounded, or it may have various degrees of flattening through either the cranial or distal portion.

1. **Smoothly curved.** Culmen rounded over entire length without any marked flattening (e.g., Probosciger, Prosopeia, Anodorhynchus); (+) curve arched (Callocephalon, Calyptorhynchus); (−) curve depressed (e.g., Amazona, Opositta);

2. **Cranially flattened—smooth.** Culmen flattened on cranial 1/4-1/3 before curving downwards without obvious angle at transition (e.g., lorikeets, Psittacus, Psittacula);

3. **Cranially flattened—angled.** Culmen flattened on cranial 1/3, before curving downwards with obvious angle and a small projection at the point of transition (e.g., Barnardiplus, Platycercus, Melopsittacus);

4. **Distally flattened.** Culmen flattened on distal 1/3 and curved cranially (Myiopsitta, Cacatua tenuirostris).

(H) **Shape of tomium (Fig. 1H)**

The outline of the tomium is assessed from the lower rear (cranial) corner forwards.

1. **Sigmoid.** The basal section is deep, before curving dorsally then ventrally towards tip (all Cacatuidae except Probosciger);

2. **Smooth.** The basal section is not much deeper than rest of tomium, which is more or less smooth (Strigops), or with a slight, gradual concavity towards tip (e.g., Trichoglossus, Polytelis, Nestor, Myiopsitta);

3. **Notched.** The basal section is not much deeper than rest of tomium, and there is a concavity before the tip. In contrast to the previous state, the cranial border of the concavity is abrupt, often creating a notched or 'toothed' appearance (e.g., Platycercus, Barnardius, Eclectus, Amazona). It is sometimes difficult in some taxa to distinguish this state from the previous one (e.g., Melopsittacus, Geoffroya);

4. **Tomium is concave overall except for a small rise near the centre (Probosciger).**

(I) **Width : length ratio (Fig. 11)**

Most parrots have rostra in which the length is more than 1 x but less than 2 x the width. There are a few exceptions in both directions.

1. Length = width (Cacatua sulphurea, Calyptorhynchus latami, approached by Psittaculirostris and Opositta);

2. Width < length < 2 x width (most psittaciforms examined);

3. Length > 2 x width (Charmosyna papou, Probosciger, Nestor, Pionites, Purpureiceps, Strigops).

(J) **Overall size (Fig. 1J)**

Scoring of overall size is a somewhat subjective assessment of the overall bulk of the rostrum, allowing for variation in shape. Specimens were placed into categories of similarly sized rostra that had some discernable discontinuities between them.

Representatives of each category were used for comparison with newly examined taxa. No quantification of these categories was made.

1. **Very small (Melopsittacus, Neophema);**
2. Small (e.g. Glossopsitta, Nympicus, Psephotus, Platycercus [smaller species and females of larger ones]);

3. Small medium (e.g. Trichoglossus, Barnardius zonarius barnardi, Platycercus caleidosonicus, Polytelis);

4. Medium (e.g. Lories, Cacatua [small species], Alisterus, Myiopsitta);

5. Large medium (e.g. Callocephalon, Euctectes, Amazona, Nestor);

6. Large (Calogryrophus, Cacatua [large species], Strigops);

7. Very large (Probosciger, Anodorhynchus, Ara).

APPENDIX II

Taxa for which the rostrum was examined

Agapornis (fisheri, lilianae, personata, roseicollis), Alisterus (scapularis), Amazona (aestiva, albifrons, amazonica, autumnales, farinosa, fimbriata, leucophala, ochrocephala, viridigenalis); Anodorhynchus (huminthinus); Aprosmictus (erythropterus); Ara (ambigua, ararauna, macao, roseicollis); Alisterus (scapularis, leucocephala, ochrocephala, viridigenalis); Anodorhynchus (huminthinus); Aprosmictus (erythropterus); Ara (ambigua, avarauna, macao, roseicollis).

APPENDIX III

Rostral characters of Australo-Papuan and selected extralimital genera of parrots

See Appendix I and Figure 1 for explanation of characters and character states. Although some states are different stages of a morpholine, overall no implication of relative polarity is intended or should be inferred. When two scores for a single character are separated by a dash (e.g. 2-3) or a comma (e.g. 4,6), it indicates that more than one state occurs among members of the genus. Parentheses around the second score (e.g. 2(1)) indicate that the condition occurs in only one species, the other members of the genus having the first score. A slash between two scores (e.g. 3/4) indicates that the state is intermediate between them and difficult to distinguish with confidence. A plus (+) or minus (−) sign following a score indicates that it is at the respective end of the state, approaching the other. Square brackets ([ ]) indicate that the character could not be evaluated on the material available.

Australasian taxa not examined are Neopsephotus, Oreopsephotus, Eunymphicus, Geopsittacus, Loriculus, Micropsitta, Psittacella and Psittichas.
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