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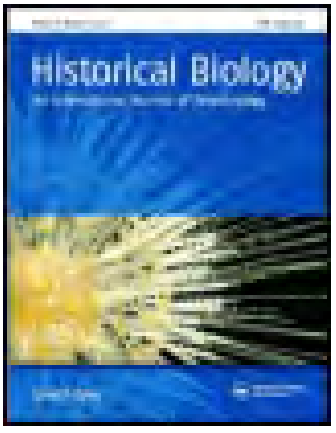

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Structure and function of the cassowary's casque and its implications for cassowary history, biology and evolution

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Structure and function of the cassowary's casque and its implications for cassowary history, biology and evolution

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Cassowaries (*Casuarius*) possess a cranial casque, sheathed by keratin and composed of modified cranial bones. We combine data and hypotheses on three areas of cassowary research. First, we present novel observations on casque anatomy. The bony core is fragile, incorporating a mass of trabeculae anteriorly and an empty space posteriorly. Secondly, we use these observations to evaluate hypotheses of casque function. Implications that the casque evolved within the context of activities involving percussive actions are unlikely and observations that might support these hypotheses are absent. It is most likely that the casque serves a sociosexual role and functions in visual and acoustic display. The similarity in casque form between males and females, combined with male parental investment, makes it plausible that the extravagant structures present in cassowaries evolved within the context of mutual sexual selection. Thirdly, we combine morphological, molecular and geological evidence to provide a new phylogenetic history for cassowaries. We suggest that cassowaries invaded New Guinea in at least two waves and provisionally regard crown–cassowaries as a geologically young, post-Pliocene clade. We provide these hypotheses as areas requiring discussion and urge other workers to test our ideas with new data on cassowary anatomy, behaviour and genetics.

Keywords: cassowaries; *Casuarius*; casques; birds; New Guinea; phylogeny

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Introduction

Cassowaries (*Casuarius*) are large, black-plumaged ratite birds, endemic to the rainforest habitats of New Guinea, Queensland and various of the Aru Islands (Rothschild 1900; Folch 1992; Davies 2002). Cassowary distribution and biogeography is complicated by the fact that people have widely traded in these bids and hence transported them beyond their natural range (a story that involves New Britain, Seram, Borneo and even further afield). Notable morphological peculiarities include their large, keratinous head casques, brightly coloured dewlaps and carunculated head and neck skin, and enlarged pedal digit II claws. Strong morphological and molecular similarities with emus (*Dromaius*) show that both taxa should be regarded as close relatives within the ratite clade Casuariiformes (Prager et al. 1976; Bledsoe 1988; Sibley and Ahlquist 1990; Lee et al. 1997; Dyke and van Tuinen 2004; Livezey and Zusi 2007; Hackett et al. 2008), although authors have differed as to whether they regard cassowaries and emus as representing distinct 'families' (Dromaiidae and Casuariidae, respectively) (Sibley and Ahlquist 1972; Cracraft 1981; Livezey and Zusi 2007) or 'subfamilies' or 'tribes' (Dromaiinae and Casuariinae, or Dromaiini and Casuariini, respectively, both included within Casuariidae) within this clade (Patterson and Rich 1987; Sibley and Ahlquist 1990; Boles 1992).

Three extant species are generally recognised within *Casuarius* (Mayr 1979; Folch 1992; Dickinson 2003; Clements 2008; Dickinson and Remsen 2013): the Double-wattled or Southern cassowary *Casuarius casuarius* Linnaeus 1758, Single-wattled cassowary *Casuarius unappendiculatus* Blythe 1860 and Dwarf or Bennett's cassowary *Casuarius bennetti* Gould 1857 (Figure 1). Each species is easily distinguished by the number or absence of wattles on the foreneck. However, the taxonomic history of the group has been volatile and more than 20 species, and substantially more subspecies, have been recognised in the recent past (Rothschild 1900; Peters 1931). At least some of these numerous 'additional' taxa surely represent valid forms: their status mostly remains untested and there is as yet no agreed-upon subspecific classification for cassowaries. One of these additional taxa – *Casuarius papuanus* Schlegel, 1871 – has recently been regarded as a valid species (Davies 2002), although note that the correct name is *Casuarius westermanni* (Perron 2011). While we have previously regarded this taxon as a subspecies of *Casuarius bennetti* (Perron 2011), the possibility that it should be recognised as a distinct species receives support from our molecular analysis: we aim to examine this further in future work. Fossil cassowaries are known from the Pliocene (Plane 1967) and Late Pleistocene of New Guinea (Rich et al.

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Figure 1. (Colour online) The three currently recognised extant cassowary species. (A) Double-wattled or Southern cassowary *Casuarius casuarius*. (B) Double-wattled cassowary in profile. (C) Single-wattled cassowary *Casuarius unappendiculatus*. (D) Dwarf or Bennett's cassowary *Casuarius bennetti*. Photographs by D. Naish and R. Perron.

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1988), and from an undetermined part of the Pleistocene of New South Wales (Lydekker 1891; Miller 1962).

While all cassowary species are mainly found in rainforest habitats, each seems to favour or be adapted to a specific elevation. *Casuarius casuarius* occurs up to 500 m, *Casuarius unappendiculatus* up to 1000 m and *Casuarius bennetti* up to 3500 m (Coates 1985; Beehler et al. 1986). In fact, these elevations may be to some degree dependent on the presence of the other species lower down.

All extant cassowaries bear a cranial casque and the group is remarkable in possessing this unique structure, formed of a keratinous sheath externally and a bony core internally. A considerable amount of curiosity and uncertainty has been expressed about the casque's structure and function, but surprisingly little has been published on its detailed anatomy. Indeed, very little is known about cassowaries in general and a substantial amount of work remains to be done on their anatomy, genetics, physiology, ecology and behaviour. This paucity of knowledge about the group – evident to anyone familiar with ratites, and well expressed in a recent book on the birds (Mack 2013) – is perhaps not obviously conveyed via the general ornithological literature, and we here hope to impress upon readers the fact that many ideas we have about these birds are still at an initial, hypothesis-building stage. The present manuscript – while presenting data on morphology, genetics and phylogeny where possible – is unashamedly speculative in places; we aim to build on our speculations and hypotheses in subsequent work, but also hope that our proposals and suggestions will promote discussion and encourage other workers to investigate, or present data on, the topics we discuss. To return to the topic of casque anatomy, the alluded to paucity of data is illustrated by the fact that Crome and Moore (1988) and Richardson (1991) represent the only published articles dedicated to this topic. We aim here to describe the detailed internal anatomy of the casque for the first time. We then discuss these structural details within the context of casque function and cassowary evolution, couching them within a novel and speculative hypothesis of cassowary history.

Casque structure

We privately obtained a *Casuarius unappendiculatus* skull, sectioned it (Figure 2), and based many of our observations on this specimen (RP, private collection). The specimen concerned was a male, c. 18 years old, kept at Ehime Tobe Zoo in Japan; its cause of death is registered as heart failure. Provenance data for the specimen prior to its arrival at the zoo do not exist, and there is no indication that the specimen is morphologically unusual relative to cassowaries in their natural state. Cassowary chicks hatch

Figure 2. (Colour online) Sectioned single-wattled cassowary *Casuarius unappendiculatus* head used in this study. Specimen from RP private collection.

with a thin, laterally compressed, sub-triangular keratinous cranial plate. The casque increases in size during ontogeny, its shape being highly variable between individuals as well as between taxa. It is variously subtriangular, rounded or trapezoidal, being tallest at a point dorsal to anywhere between the orbit and quadrate (Figures 2 and 3(A)). We are not aware of work that precisely determines the homology or identity of the bones involved in casque formation. However, an image of a scanned cassowary embryo produced by WitmerLab at Ohio University (and available online: http://www.oucom.ohiou.edu/dbms-witmer/3D-Visualization.htm) reveals the presence of distinct thickenings on each of the frontal bones, suggesting that the casque primarily represents novel hypertrophy of these bones. A study of casque ontogeny is sorely needed. Anteriorly, the bony crest extends well anterior to the base of the rostrum, overlapping and fusing with the posterodorsal ramus of the premaxilla. Despite major differences in shape and size, the casque is intrinsically the same across all species. The differences in casque form observed across all cassowary species relate to ontogeny (older, adult individuals typically having larger casques than juveniles and younger adults) but perhaps to sex and adaptation to

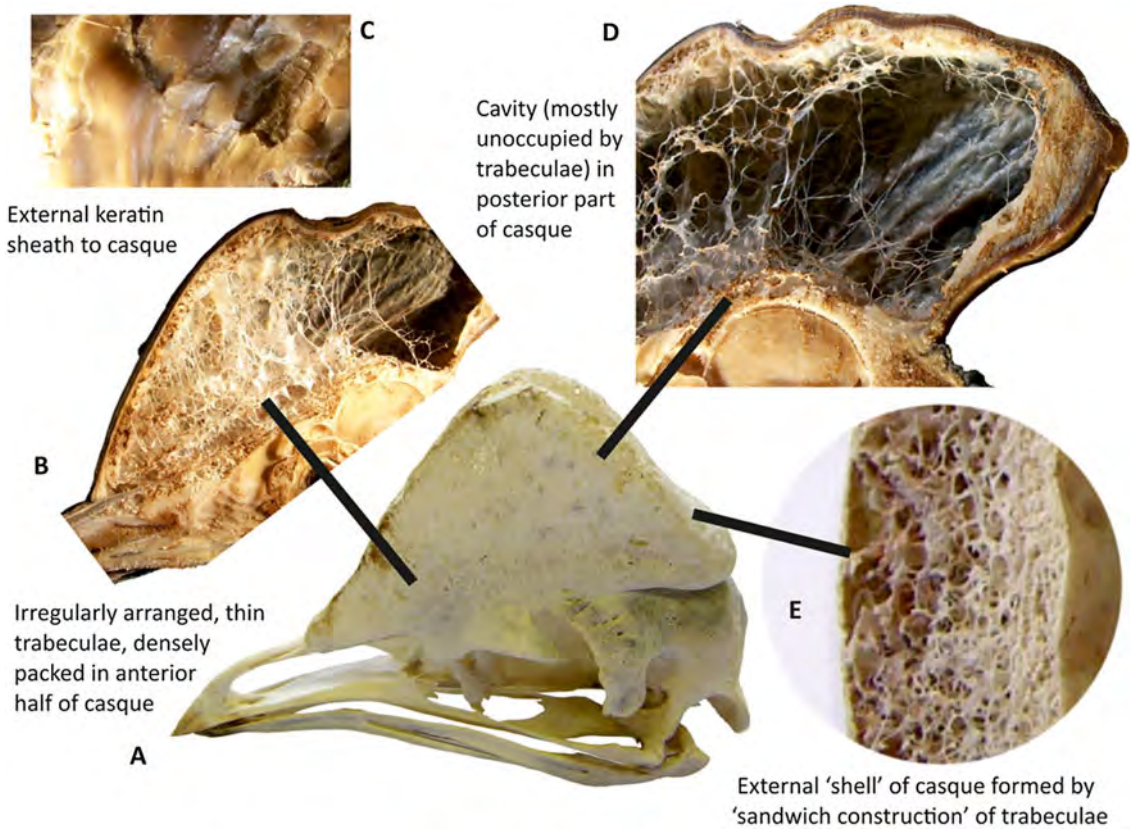

Figure 3. (Colour online) External and internal details of the cassowary casque. (A) Complete skull of *Casuarius bennetti* (the cassowary with the lowest casque and the only one where the casque is ordinarily subtriangular in profile). (B) Anterior part of interior of sectioned casque of *Casuarius unappendiculatus* specimen shown in Figure 2, anterior to the left. (C) External keratinous sheath of casque of *Casuarius unappendiculatus* specimen shown in Figure 2, showing flaked, cracked surface of the sort typically seen in live birds. (D) Posterior part of interior of sectioned casque of *Casuarius unappendiculatus* specimen shown in Figure 2, anterior to the left. (E) 'Sandwich layer' at edge of casque.

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local conditions. We also assume (based on the appearance of individuals kept in captivity) that casque size and shape reflect health and diet, individuals of 'better quality' apparently having larger, taller casques. Without the dermis and epidermis that form the keratinous outer sheath of the casque, it is a lightweight, fragile structure that can be damaged easily through clumsy handling. The keratinous sheath is sometimes damaged or partially worn. The keratin surface of the specimen we examined revealed some minor regions of flaking and cracking, as is typical for captive and wild cassowaries. However, wear or damage that might be informative with respect to the behavioural hypotheses discussed below was not evident.

Internally, the casque is occupied by a loosely knit web of irregularly arranged, sparse, extremely thin trabeculae: these are most densely packed in the anterior half of the casque (Figure 3(B)) but are absent posteriorly where a cavity is present (Figure 3(D)). Surrounding the internal mass of trabecular fibres is a bony shell composed of denser bone, the external surface of which is marked with foramina and shallow, dorsoventrally aligned, divaricating canals for the reception of blood vessels and nerves; Richardson (1991) described these as up to 1 mm deep and nothing appears unusual about their number, density or arrangement compared with the similar bony canals present on the keratin-covered cranial bones (premaxillae especially) seen in other birds.

The shell-like outer layer of the casque is approximately 2–3 mm thick and formed of thousands of tiny cells formed by fine strut-like trabeculae arranged in a semi-regular, honeycomb-like arrangement (Figure 3(E)), all enclosed within inner and outer bone layers, the overall effect being that of a 'sandwich' of bone cells. In places, the cells are arranged in rows that are approximately parallel to the inner and outer layers. Similar 'sandwich' layers formed of parallel rows of cells have been figured for other birds where the rows may be double, four-deep or more randomly arranged (Bühler 1988). This arrangement is best known for the braincase bones of passerines but occurs widely, including in the palate, sternum and the ends of long bones (Bühler 1988). The dermis and epidermis are in tight contact with the bony core of the casque, the soft tissues together forming a keratinous sheath over the skeletal component. The entire external sheath of the casque is stiff along its anterior and dorsal edges but soft and pliable elsewhere: it is not a hard 'helmet', but flexible and able to deform when subjected to load (Crome and Moore 1988; Richardson 1991).

Descriptions have differed in their interpretation of casque contents. Jones et al. (2003) noted that the casque seemingly contains liquid of some kind; Crome and Moore (1988) referred to the presence of 'a core of firm, cellular foam-like material that looks like some hi-tech plastic' (p. 123); while Richardson (1991) referred to the presence of 'large amounts of darkly pigmented sludge [that came] from the deeper regions of the casque', indicating the presence of 'an extensive vascular network and possibly other structures deep within the casque' (p. 57). Richardson (1991) presumed that the method of preparing the skull was somehow responsible for the 'sludge'. Our observations of cassowary dissections lead us to conclude that reports of liquid or sludge present between the bony core and the keratinous casque in fact refer to blood that has haemorrhaged from vessels associated with the dermis: it is extremely easy to damage the outer layer of the bony casque due to its fragility. The casque is not occupied internally by liquid and contains only those visible filaments. This discovery allows us to examine the list of potential purposes in a new light.

Casque function

Six hypotheses have been put forward to explain the evolution and function of the cassowary casque, typically pertaining to the best known species, *Casuarius casuarius*. Note that we have only heard some of the purported functions reported in anecdotal fashion and are not aware of their serious proposal in the literature: for the obvious sake of completeness, we include them here anyway. We note, in addition, that the casque has been shown to play a role in heat dissipation (Phillips and Sanborn 1994); because this role is similar in importance to that occurring across exposed parts of the skin, it is likely incidental and a specialised thermoregulatory role for the casque has not been suggested to our knowledge. We here discuss each proposal and evaluate it within the context of our new data on casque structure.

1. *Sexual ornamentation.* The possibility that the casque functions in display, that it is used as an indicator of fitness and that it hence evolved under sexual selection pressure is plausible, especially given unconfirmed indications that casque height is sexually dimorphic. It may not be adequately appreciated how little is known about cassowary behaviour in the wild: we are not aware of useful data that have been reported on how the casque might function in sociosexual terms, nor have adequate measurements yet been published on casque dimensions or variability. It is one of our aims that relevant data be collected and appropriate analysis be carried out in time.

2. *Weapon used in intraspecific combat.* The possibility that the casque is used in intraspecific combat, presumably in disputes over territory or access to mates, has been considered. To our knowledge, observational data supporting this possibility have not been reported. The relatively light and fragile construction of the crest strongly suggests that a role in combat should be considered extremely unlikely. Furthermore, we regard it as far more likely that intraspecific disputes between cassowaries involve kicking and jabbing with the feet, as is typical for ratites.

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3. *Moving foliage and detritus on the rainforest floor.* We are aware of one published observation describing use of the casque to move leaf litter during foraging (Folch 1992). While, as noted above, surprisingly little observational data on wild cassowaries have been published, the rarity of this behaviour, combined with the position and form of the structure, indicates that regular use of the casque (enough to exert a major selective pressure during evolution) in this fashion is unlikely.

4. *For knocking hanging branches to dislodge fruit.* It has been suggested that the casque is used as a tool for the dislodging of fruit, with some people even suggesting that the form of the *Casuarius bennetti* casque results from habitual use of the structure in foraging of this sort. We are not aware of observational data that might support this suggestion. Furthermore, as with the previous suggestion, there is no obvious indication from casque form or position that it might be regularly used in this fashion; not regularly enough to exert selective pressure during evolution, anyway. Again, the relative fragility of the casque argues against the idea that it could be regularly used in a vigorous activity like branch-knocking.

5. *For cranial protection when charging through undergrowth.* Suggestions that the casque functions as head protection were favoured by Crome and Moore (1988) who proposed that the 'foam' they regarded as forming the internal contents of the casque's core provided shock-absorbing qualities. Again, observational data that might support this possible role for the casque have not been reported to our knowledge, nor does the casque appear robust enough or tough enough to serve a useful role in head protection.

6. *As a resonance box in low frequency communication.* Although the most recently mooted purpose, we propose that this is most likely the primary one. It is reasonably well documented that cassowaries produce low-frequency vocalisations (Jones et al. 2003). During the mating season – the only time the normally solitary, territorial (Bentrupperbäumer 1992) cassowaries are amenable to contact with members of their own species – cassowaries perform ritualised dances with members of the opposite sex. During these interactions, deep, guttural, low-frequency (20–30 Hz) sounds (Jones et al. 2003) are emitted. A vocalising bird lowers its head such that the casque is held pointing towards the partner (RP, personal observation). We suggest that this behaviour represents use of the casque in directing vocalisations towards a partner, the possibility then existing that casque size and form are intrinsically linked to vocal signalling and hence to the advertising of fitness; such a role suggests that sexual selection has driven casque evolution in these birds.

Tropical rainforests can be very dense places where vision is limited and sound does not travel very well. Low-frequency sound has a much greater range, a fact exploited by elephants and cetaceans and, among birds, by emus and cassowaries. Emus inflate and then compress their cervical air sac and long tracheal pouch: a small opening in the ventral wall of the latter facilitates the creation of these calls (Eastman 1969). Whereas the emu does not have a casque, it lives in open environments where both vision and sound are relatively undisturbed. Again, hard data on cassowary vocalisations and acoustics are not currently available (we are not aware of suitable recordings from the wild, or from captive specimens, that are available for analysis) but there are indications from tracheal anatomy (Forbes 1881) that cassowaries and emus are similarly equipped and capable of the same sorts of vocalisations. Rothschild noted that 'The voice of the cassowaries is a curious sort of snorting, grunting, and bellowing, usually not very loud, and differing according to the species'. The use of vocal signals by cassowaries both warns intruders and notifies availability during the mating season. However, Starck (1995) suggested that cavernous subdermal blood sinuses may play a role in the amplification of the booming noises made by cassowaries, raising the question as to whether these structures operate in conjunction with the crest during vocalisation, or indeed whether these sinuses take over the proposed acoustic function of the casque entirely. Further work is needed to determine which structures are used in amplification, if either of them is.

Cassowary evolution: a speculative scenario

We propose the following hypothesis as a possible explanation for cassowary casque evolution and for its variation in size and form. We recognise that this model is unavoidably speculative and cannot be fully evaluated due to a scarce fossil record that provides little data on the casque morphology of ancient cassowary taxa. Nevertheless, we propose this hypothesis as our best explanation for the phylogeny and behavioural and morphological variation discovered in these birds and aim to build on it in future studies.

Fossils from the Pliocene and Pleistocene indicate that small, *Casuarius bennetti*-sized cassowaries, mostly referred to the problematic taxon *C. lydekkeri* and not demonstrably related to any of the extant taxa, were present in New Guinea and Australia during the Pliocene and Pleistocene (Lydekker 1891; Miller 1962; Plane 1967; Rich et al. 1988). There is no indication of close affinity between these fossil forms and living cassowaries. Furthermore, they lack characters common to the extant taxa, possessing a shallower, narrower pelvis, more gracile femur and a narrower proximal end to the tarsometatarsus (Rich et al. 1988). Based on this distribution of characters, we hypothesise that they are outside the clade that includes the extant taxa and thus that crown–cassowaries are a post-Pliocene clade.

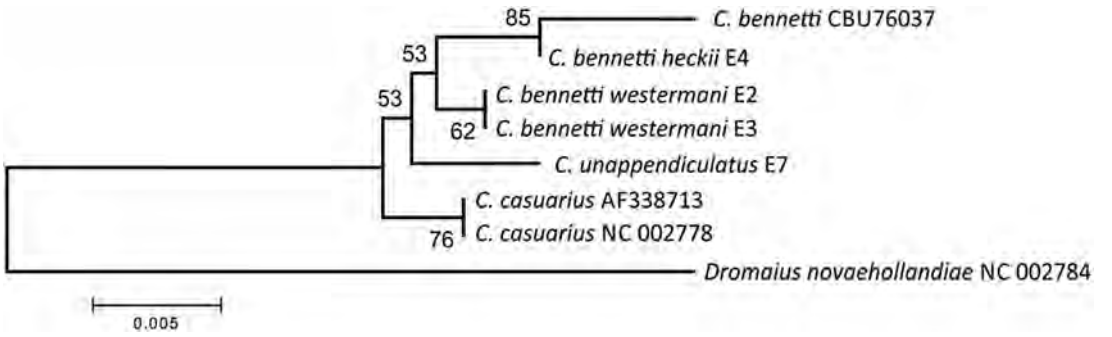

Figure 4. Phylogeny generated from DNA sequences of eight cassowary specimens and one emu (see Appendix). The genetic distance present between *Casuarius bennetti westermanni* and other specimens included in *Casuarius bennetti* is consistent with the view that *Casuarius bennetti westermanni* should be recognised as a valid taxon (Perron 2011).

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Over the past several years, we have collected mtDNA data from numerous cassowary individuals belonging to seven extant taxa (RP, unpublished data): the full extent and results of this study will be presented elsewhere and only a preliminary assessment is included here (Figure 4; Appendix). These data indicate that *Casuarius casuarius* is the sister taxon to remaining extant cassowaries. Furthermore, both the Oligo-Miocene fossil *Emuarius* and extant emus are Australian, suggesting that crown–cassowaries originated in Australia. A divergence date of 20–25 million years was suggested for the cassowary–emu lineages by Sibley and Ahlquist (1990), and 35–38 million years was suggested by Cooper et al. (2001). If *Emuarius guljaruba* from the Upper Oligocene Etadunna Formation of South Australia truly is an emu as argued by Boles (2001), most of cassowary (and emu) evolution occurred after this time (*Emuarius* appears to be close to the time of emu–cassowary divergence). Little is known about the habitat preferences or ecomorphology of extinct cassowaries, but it is assumed that these taxa were rainforest-adapted.

Given that casques are absent in emus and other ratites, the casque is assumed to be a novelty that evolved after the divergence of the cassowary lineage from the cassowary–emu common ancestor. The problems of communication within a rainforest were alluded to above. Although cassowaries are good swimmers, their distribution in New Guinea (and at least some of the surrounding islands) is almost certainly explained either by vicariance or by the use of terrestrial land-bridges that existed during times of low sea level (Figure 5). New Guinea has a complex geological history and essentially consists of a mostly central-southern and western Australian continental craton in addition to a large number (over 30) of terranes (some of which are of continental origin) that form the central-northern and eastern regions. These accreted during various parts of the Oligocene, Miocene and Pliocene (and perhaps during the Eocene as well) (Pigram and Davies 1987; Polhemus and Polhemus 1998), the docking of several of the larger terranes during the middle or late Oligocene probably causing the New Guinea Orogeny that initiated at this time (Pigram and Davies 1987). Given the distribution of emus and the fossil occurrence of cassowaries on mainland Australia (Lydekker 1891; Miller 1962; Plane 1967; Boles 2001), our primary assumption is that cassowaries are of Australian ancestry,

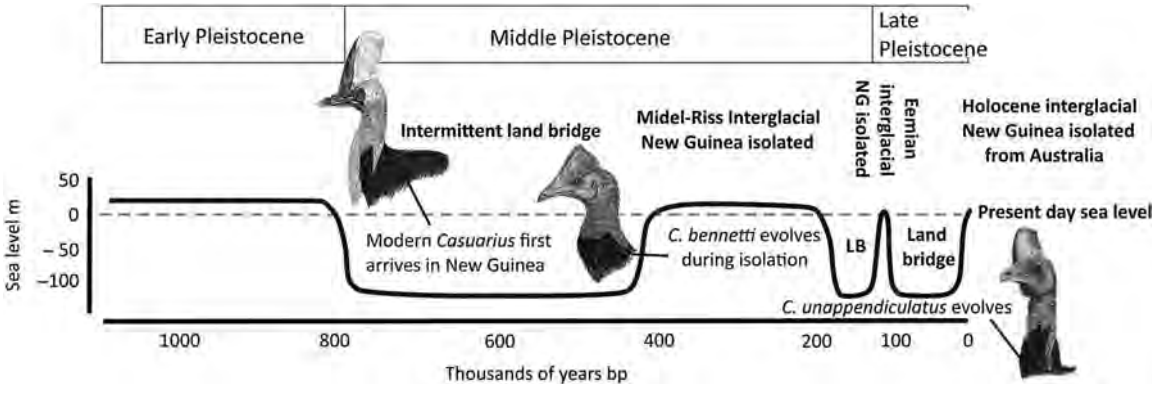

Figure 5. Speculative scenario linking cassowary evolutionary history to changing sea level and the emergence and submergence of terrestrial connections between New Guinea and Australia.

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in which case any vicariance-based hypothesis of their distribution must link their presence on New Guinea with the separation of the northern part of the Australian continental craton from the remainder of Australia.

So far as we can tell at present (a poor fossil record on New Guinea being a primary limitation), the controlling factor as goes the movement of terrestrial animals between Australia and New Guinea is sea level, the high sea levels of the Miocene and Pliocene seemingly preventing the terrestrial migration of large animals: indeed, it appears that New Guinea was mostly drowned during the Miocene (Dow and Sukamto 1984). In view of this, it has generally been assumed that terrestrial vertebrate taxa shared between Australia and New Guinea split during the Pleistocene – in other words, that any taxon endemic to New Guinea is geologically very young. However, a growing number of molecular studies have proposed that terrestrial snakes (Kuch et al. 2005), birds (Joseph et al. 2001), mammals (Rowe et al. 2008; Malekian et al. 2010; Meredith et al. 2010; Macqueen et al. 2011) and other vertebrates moved between Australia and New Guinea during the Pliocene or even the Late Miocene. While we remain open to the possibility that crown–cassowaries migrated to New Guinea during the Pliocene or Miocene, the fact that the same species of cassowary – *Casuarius casuarius*, the sister-taxon of other crown–cassowaries (Figure 4) – occurs on Australia as well as New Guinea leads us to hypothesise that the movement of crown–cassowaries to New Guinea occurred during the Pleistocene. This is because tetrapod species common to both regions evolved during the Pleistocene (e.g. Aplin and Ford 2014) and because sister-species within clades that are common to both areas diverged during the Pleistocene (e.g. Hocknull et al. 2007; Bryant et al. 2011; Rowe et al. 2011; Aplin and Ford 2014). Furthermore, we assume that *Casuarius casuarius* is the oldest extant cassowary species based on its phylogenetic position relative to other crown–cassowaries. We hope to see these contentions tested in future work.

At which point during the Pleistocene might cassowaries have dispersed to New Guinea? The first period when sea level was sufficiently low to allow terrestrial crossing lasted nearly 400,000 years (Chappell 1974; Chappell et al. 1996) and we suggest that *Casuarius casuarius* extended its range during this time to include the southern half of present day New Guinea. When sea level rose during the Mindel–Riss interglacial, this population was stranded on New Guinea, then evolving in isolation for the following 200,000 years (Figure 5).

We suggest that it was during this period of isolation that the population concerned became genetically different and specialised for New Guinea's physical and botanical environment. Several key events occurred during this period of isolation: the mountains of central New Guinea became considerably higher, perhaps by 700 m or more (Audley-Charles and Hallam 1988), and the influence of Asian botanical flora, particularly on the northern side, increased in significance (Adam 1992). During the next period of lowered sea level, New Guinea was invaded by members of the Australian population of *Casuarius casuarius*: while probably still able to interbreed with the previously isolated group, we suggest that members of both populations would now have inhabited distinct habitats. The now endemic New Guinea cassowary had, to some extent, adapted to local conditions and could utilise more of the available habitat (most notably those at higher elevation) than the Australian invaders. At some time in the last 200,000 years, *Casuarius bennetti* has become genetically and morphologically distinct from other extant cassowaries. It is the only cassowary able to inhabit elevations as high as 3500 m and dwell at sea level without ill effects (RP, unpublished data). In the wild, it is probably unable to interbreed with *Casuarius casuarius*.

Intriguingly, individuals of *Casuarius unappendiculatus* exhibit casque variation that seems to span the morphological 'distance' in casque form between *Casuarius casuarius* and *Casuarius bennetti*. It may not be coincidental that *Casuarius unappendiculatus* frequents altitudes also intermediate between those frequented by these two species. We consider it plausible that *Casuarius unappendiculatus* occupies an ecomorphological niche 'intermediate' between the other species – a possibility consistent with its phylogenetic position (Figure 4; Appendix); indeed, it may even interbreed with both *Casuarius casuarius* and *Casuarius bennetti* in the wild. The phylogenetic relationships of these species, and the possible timescale of their evolution, will be explored more fully elsewhere.

Conclusions and areas for future work

A surprising dearth of published data on cassowary casque anatomy partly motivated us to publish this work. We recognise that more detailed analyses should be published in future but, meanwhile, have established some basic parameters of casque anatomy. The casque is not liquid-filled or occupied by a consistent foam-like material but, instead, filled internally with a mass of fine trabeculae anteriorly and an air-filled cavity posteriorly. We are aware of six hypotheses that aim to present the main selective force behind the casque's evolution, all speculative and untested or under-tested: we reject those that seem inconsistent with the position and relatively delicate anatomy of the casque (e.g. that it evolved under selective pressure related to use of the casque in overturning leaf litter, or knocking or banging vegetation). The idea that the casque is used as a visual signal in sociosexual display, and as an acoustic organ that similarity is important in social and sexual terms, seems most consistent with casque anatomy. Preliminary data supporting the acoustic function have been published

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(Jones et al. 2003; Mack and Jones 2003) and our additional data support it (RP, unpublished data). Behavioural work on use of the casque as a sexual display structure is needed. We note that this will be of broad interest with respect to the evolution of extravagant structures in birds and other archosaurs, because a major area of debate concerns whether the superficially similar bony cranial structures of Mesozoic dinosaurs evolved within the context of sexual display or as species identification badges (Hone and Naish 2013; Padian and Horner 2014). As discussed above, extant cassowary species are separated by altitude, rendering it unlikely that a role in 'species recognition' exerted a selective pressure on casque evolution (the concept that extravagant structures have evolved within the context of a role in species recognition is highly problematic in any case: see Hone and Naish 2013). Furthermore, data suggest that hybridisation between morphologically distinct cassowary species (*Casuarius casuarius* and *Casuarius unappendiculatus*, and *Casuarius unappendiculatus* and *Casuarius bennetti*) occurs on occasion in the wild – an observation at odds with the idea that extravagant cranial structures specifically exist such that populations distinguish themselves from others and hence avoid breeding with them.

Furthermore, the fact that male and female cassowaries are similarly ornamented with large casques (they exhibit *elaborate monomorphism*) makes it likely that, whatever the casque's function, members of both sexes are using it in similar ways. Elsewhere within birds, the possession of extravagant display structures in both males and females is plausibly explained by mutual sexual selection: the phenomenon in which members of both sexes evaluate potential partners on the basis of fitness and quality. Mutual sexual selection is best known for certain grebes, auks, swans and starlings (Huxley 1914; Jones and Hunter 1993; Kraaijeveld, Gregurke, et al. 2004; Kraaijeveld, Carew, et al. 2004; Komdeur et al. 2005), but the presence of elaborate display structures, patterns and colours in both the males and females of many additional taxa have led to suggestions that it might be more widespread than currently realised (Jones 1992). Mutual sexual selection is far from restricted to birds, also being documented in insects (Chenoweth and Blows 2003; South and Arnqvist 2011), pipefishes (Widemo 2003), sticklebacks (Bergstrom and Real 2000) and iguanian lizards (Ord and Stuart-Fox 2006). Its prevalence in extant birds and other animals has in fact inspired palaeontologists to propose it as a viable explanation for the presence of extravagant structures in both the males and females of Mesozoic dinosaurs and pterosaurs (Hone et al. 2011). The extensive role that male cassowaries play in parental care suggests that males may exhibit a high degree of selectivity with respect to female partners (Amundsen 2000); in other words, we consider it plausible that mutual sexual selection may be at play in these birds. We thus propose this as an additional hypothesis that can only be supported or refuted with the collection of field data on cassowary social and reproductive behaviour. We are aware that mutual sexual selection may not always explain the presence of elaborate monomorphism (Tarvin and Murphy 2012; van Rooij and Griffith 2012).

Morphological characters suggest that the poorly known fossil cassowaries of the Pliocene and Pleistocene (the taxonomy of which is confused: use of the name *Casuarius lydekkeri* for these taxa is provisional and may be technically incorrect) are outside the clade that includes the extant species. This requires confirmation through detailed analysis, although the incomplete nature of the fossil remains constrains examination at this point. New fossils that help populate the long cassowary ghost lineage are needed for us to better understand the evolution of these birds. Within living cassowaries, we propose a new phylogenetic hypothesis that we aim to test and examine in subsequent work.

We hope that future work examining and testing several of the hypotheses and speculations mentioned or explored here will be undertaken, and that the data required to test them will be collected. The following areas could be regarded as the focus for future work: What is the status and validity of the more distinctive cassowary subspecies – are they valid taxa, hybrids, artificially introduced populations or representatives of intraspecific variation? Does the casque convey information on maturity, sexual status and fitness, and is it used as a sociosexual signal? Is the casque used in the same manner in both male and female cassowaries, and is mutual sexual selection at play? Finally, can the detailed anatomical structure of the cassowary casque, described and illustrated here for the first time, be linked to selection associated with any of the special functions proposed for this structure?

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Note

1. Email: casuarius2006@yahoo.co.uk

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Appendix

MtDNA sequences coded for seven cassowary specimens and one emu used in this study. Further discussion and data on additional specimens will be presented in a future study. Four sequences listed here (CBU76037, AF338713, NC_002778 and NC_002784) are available via Genbank; others (E2–E7) are novel and will be discussed in a future study. Abbreviations: C. b., *Casuarius bennetti*; C. c., *Casuarius casuarius*; C. b. w., *Casuarius bennetti westermanni*; C. b. h., *Casuarius bennetti hecki*; C. u., *Casuarius unappendiculatus*; D. n., *Dromaius novaehollandiae*.

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C. b._CBU76037                  AAGGAACTAGGCAAACCTAAGGCCCGACTGTTTACCAAAAACATAGCCTT
C. c._AF338713                  AAGGAACTAGGCAAACCTAAGGCCCGACTGTTTACCAAAAACATAGCCTT
C. c._NC_002778                 AAGGAACTAGGCAAACCTAAGGCCCGACTGTTTACCAAAAACATAGCCTT
C. b. w._E2                     ??????????????????????????????????CAAAAACATAGCCTT
C. b. w._E3                     ??????????????????????????????????CAAAAACATAGCCTT
C. b. h._E4                     ????????????????????????????????????????GCCTT
C. u._E7                        ??????????????????????????????????????????????
D. n._NC_002784                 AAGGAACTAGGCAAACCAAAGGCCCGACTGTTTACCAAAAACATAGCCTT

C. b _CBU76037                  CCAGCTAGCAACAAGTATTGAAGGTGATGCCTGCCCAGTGACTTATGTTCA
C. c._AF338713                  CAGCTAACAACAAGTATTGAAGGTGATGCCTGCCCAGTGACTTATGTTTA
C. c._NC_002778                 CAGCTAACAACAAGTATTGAAGGTGATGCCTGCCCAGTGACTTATGTTTA
C. b. w._E2                     CAGCTAGCAACAAGTATTGAAGGTGATGCCTGCCCAGTGACTTATGTTTA
C. b. w._E3                     CAGCTAGCAACAAGTATTGAAGGTGATGCCTGCCCAGTGACTTATGTTTA
C. b. h._E4                     CAG?TAGCAACAAGTATTGAAGGTGATGCCTGCCCAGTGACTTATGTTCA
C. u._E7                        ????TA?CAACAAGTATTGAAGGTGATGCCTGCCCAGTGACTTACGTTTA
D. n._NC_002784                 CAGCTAACAACAAGTATTGAAGGTGATGCCTGCCCAGTGACTTATGTTTA

C. b _CBU76037                  ACGGCCGCGGTATCCTAACCGTGCGAAGGTAGCGCAATCAATTGTCCCAT
C. c._AF338713                  ACGGCCGCGGTATCCTAACCGTGCGAAGGTAGCGCAATCAATTGTCCCAT
C. c._NC_002778                 ACGGCCGCGGTATCCTAACCGTGCGAAGGTAGCGCAATCAATTGTCCCAT
C. b. w._E2                     ACGGCCGCGGTATCCTAACCGTGCGAAGGTAGCGCAATCAATTGTCCCAT
C. b. w._E3                     ACGGCCGCGGTATCCTAACCGTGCGAAGGTAGCGCAATCAATTGTCCCAT
C. b. h._E4                     ACGGCCGCGGTATCCTAACCGTGCGAAGGTAGCGCAATCAATTGTCCCAT
C. u._E7                        ACGGCCGCGGTATCCTAACCGTGCGAAGGTAGCGCAATCAATTGTCCCAT
D. n._NC_002784                 ACGGCCGCGGTATCCTAACCGTGCGAAGGTAGCGCAATCAATTGTCCCAT

C. b _CBU76037                  AAATCGAGACTTGTATGAATGGCTAAACGAGGTCTTAACTGTCTCTTGCA
C. c._AF338713                  AAATCGAGACTTGTATGAATGGCTAAACGAGGTCTTAACTGTCTCTTGCA
C. c._NC_002778                 AAATCGAGACTTGTATGAATGGCTAAACGAGGTCTTAACTGTCTCTTGCA
C. b. w._E2                     AAATCGAGACTTGTATGAATGGCTAAACGAGGTCTTAACTGTCTCTTGCA
C. b. w._E3                     AAATCGAGACTTGTATGAATGGCTAAACGAGGTCTTAACTGTCTCTTGCA
C. b. h._E4                     AAATCGAGACTTGTATGAATGGCTAAACGAGGTCTTAACTGTCTCTTGCA
C. u._E7                        AAATCGAGACTTGTATGAATGGCTAAACGAGGTCTTAACTGTCTCTTGCA
D. n._NC_002784                 AAATCGAGACTTGTATGAATGGCTAAACGAGGTCTTAACTGTCTCTTGCA

C. b _CBU76037                  GATAATCAATGAAATTGATCTTCC-GTGCAAAAGCAGGAATATGAGCATAA
C. c._AF338713                  GATAATCAGTGAAATTGATCTTCCTGTGCAAAAGCAGGAATATGAACATAA
C. c._NC_002778                 GATAATCAGTGAAATTGATCTTCCTGTGCAAAAGCAGGAATATGAACATAA
C. b. w._E2                     GACAATCAATGAAATTGATCTTCCTGTGCAAAAGCAGGAATATGAACATAA
C. b. w._E3                     GACAATCAATGAAATTGATCTTCCTGTGCAAAAGCAGGAATATGAACATAA
C. b. h._E4                     GATAATCAATGAAATTGATCTTCCTGTGCAAAAGCAGGAATATGAGCATAA
C. u._E7                        GATAATCAATGAAATTGATCTTCCTGTGCAAAAGCAGGAATATGAACATAA
D. n._NC_002784                 GATAATCAGTGAAATTGATCTTCCTGTGCAAAAGCAGGAATATGGACATAA

C. b _CBU76037                  GACGAGAAGACCCTGTGGAACTTTAAAATCAAGGACCAATGCACTCAACT
C. c._AF338713                  GACGAGAAGACCCTGTGGAACTTAAAAATCAAGGACCAATGCACTCAACT
C. c._NC_002778                 GACGAGAAGACCCTGTGGAACTTAAAAATCAAGGACCAATGCACTCAACT
C. b. w._E2                     GACGAGAAGACCCTGTGGAACTTAAAAATCAAGGACCAATGCACTCAACT
C. b. w._E3                     GACGAGAAGACCCTGTGGAACTTAAAAATCAAGGACCAATGCACTCAACT
C. b. h._E4                     GACGAGAAGACCCTGTGGAACTTAAAAATCAAGGACCAATGCACTCAACT
C. u._E7                        GACGAGAAGACCCTGTGGAACTTAAAAATCAAGGACCAATGCACTCAACT
D. n._NC_002784                 GACGAGAAGACCCTGTGGAACTTAAAAATCGAGGACCAATGCATTTAACT
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(*Continued*)

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C. b _CBU76037                  TCCAAACCTACCAAGGTTCACTTCATCTGCAGCAATGGTCCCCATTTTTC
C. c._AF338713                  TCCAAACCTACCAAGGTTCACTTCATCTGCAGCAATGGTCCTCATTTTTC
C. c._NC_002778                 TCCAAACCTACCAAGGTTCACTTCATCTGCAGCAATGGTCCTCATTTTTC
C. b. w._E2                     TCCAAACCTACCAAGGTTCACTTCATCTGCAGCAATGGTCCCCATTTTTC
C. b. w._E3                     TCCAAACCTACCAAGGTTCACTTCATCTGCAGCAATGGTCCCCATTTTTC
C. b. h._E4                     TCCAAACCTACCAAGGTTCACTTCATCTGCAGCAATGGTCCCCATTTTTC
C. u._E7                        TCCAAACCTACCAAGGTTCACTTCATCTGCAGCAATGGTCCTCATTTTTC
D. n._NC_002784                 TCCGAACCTACTGAGGCTCACTTTATATGCAATAATGGTCCCTATTTTTC

C. b _CBU76037                  GGTTGGGGCGACCTTGGAGAAAAGAAGATCCTCCAAAAATAAGACCATTA
C. c._AF338713                  GGTTGGGGCGACCTTGGAGGAAAGAAGATCCTCCAAAAATAAGACCATTA
C. c._NC_002778                 GGTTGGGGCGACCTTGGAGGAAAGAAGATCCTCCAAAAATAAGACCATTA
C. b. w._E2                     GGTTGGGGCGACCTTGGAGAAAAGAAGATCCTCCAAAAATAAGACCATTA
C. b. w._E3                     GGTTGGGGCGACCTTGGAGAAAAGAAGATCCTCCAAAAATAAGACCATTA
C. b. h._E4                     GGTTGGGGCGACCTTGGAGAAAAGAAGATCCTCCAAAAATAAGACCATTA
C. u._E7                        GGTTGGGGCGACCTTGGAGAAAAAGAAGAACCTCCAAAAATAAGACCATTA
D. n._NC_002784                 GGTTGGGGCGACCTTGGAGAAAAAAGAATCCTCCAAAAATAAGACCATAA

C. b _CBU76037                  ATCTTGACTAAGAACTACACCTCAAAGTACTAACAGTAACCAGACCCAAT
C. c._AF338713                  ATCTTGACTAAGAACTACACCTCAAAGTACTAACAGTAACCAGACCCAAT
C. c._NC_002778                 ATCTTGACTAAGAACTACACCTCAAAGTACTAACAGTAACCAGACCCAAT
C. b. w._E2                     ATCTTGACTAAGAACTACACCTCAAAGTACTAACAGTAACCAGACCCAAT
C. b. w._E3                     ATCTTGACTAAGAACTACACCTCAAAGTACTAACAGTAACCAGACCCAAT
C. b. h._E4                     ATCTTGACTAAGAACTACACCTCAAAGTACTAACAGTAACCAGACCCAAT
C. u._E7                        ATCTTGACTAAGAACTACACCTCAAAGTACTAACAGTAACCAGACCCAAT
D. n._NC_002784                 ACCTTAACTAAGAACCACACCTCAAAGTACTAACAGTAACCAGACCCAAT

C. b _CBU76037                  ATAATTGATTAATGAACCAAGCTACCCCAGGGATAACAGCGCAATCTCCT
C. c._AF338713                  ATAATTGATTAATGAACCAAGCTACCCCAGGGATAACAGCGCAATCTCCT
C. c._NC_002778                 ATAATTGATTAATGAACCAAGCTACCCCAGGGATAACAGCGCAATCTCCT
C. b. w._E2                     ATAATTGATTAATGAACCAAGCTACCCCAGGGATAACAGCGCAATCTCCT
C. b. w._E3                     ATAATTGATTAATGAACCAAGCTACCCCAGGGATAACAGCGCAATCTCCT
C. b. h._E4                     ATAATTGATTAATGAACCAAGCTACCCCAGGGATAACAGCGCAATCTCCT
C. u._E7                        ATAATTGATTAATGAACCAAGCTACCCCAGGGATAACAGCGCAATCTCCT
D. n._NC_002784                 ATAATTGATTAATGAACCAAGCTACCCCAGGGATAACAGCGCAATCTCCT

C. b _CBU76037                  TCAAGAGCCCATATCGACAAGGAGGTTTACGACCTCGATGTTGGATCAGG
C. c._AF338713                  TCAAGAGCCCATATCGACAAGGAGGTTTACGACCTCGATGTTGGATCAGG
C. c._NC_002778                 TCAAGAGCCCATATCGACAAGGAGGTTTACGACCTCGATGTTGGATCAGG
C. b. w._E2                     TCAAGAGCCCATATCGACAAGGAGGTTTACGACCTCGATG?TGGATCAGG
C. b. w._E3                     TCAAGAGCCCATATCGACAAGGAGGTTTACGACCTCGATG?TGGATCAGG
C. b. h._E4                     TCAAGAGCCCATATCGACAAGGAGGTTTACGACCTCGATGTTGGATCAGG
C. u._E7                        TCAAGAGCCCATAT?GACAAGGAGGTTTACGACCTCGATGTTGGATCAGG
D. n._NC_002784                 TCAAGAGCCCATATCGACAAGGAGGTTTACGACCTCGATGTTGGATCAGG

C. b _CBU76037                  ACATCCTAATGGTGCGCCCGCTATTAAGGGTTCGTTTGTTCAACGATTAA
C. c._AF338713                  ACATCCTAATGGTGCAGCCGCTATTAAGGGTTCGTTTGTTCAACGATTAA
C. c._NC_002778                 ACATCCTAATGGTGCAGCCGCTATTAAGGGTTCGTTTGTTCAACGATTAA
C. b. w._E2                     ACATCCTAATGGTGCAGCCG??????????????????????????????
C. b. w._E3                     ACATCCTAATGGTGCAGCCG??????????????????????????????
C. b. h._E4                     ACATCCTAATGGTGCAGCCGCTATTAAGGGTTCGTTTGTTCAACGATTAA
C. u._E7                        ACATCCTAATGGTGCAGCCGCTATTAAGGGTTCGTTTGTTCAACGATTAA
D. n._NC_002784                 ACATCCTAATGGTGCAGCCGCTATTAAGGGTTCGTTTGTTCAACGATTAA

C. b _CBU76037                  TAGTCCTACGTGATCTGAGTTCAGACCGGAGCAATCCAGGTCGGTTTCTA
C. c._AF338713                  TAGTCCTACGTGATCTGAGTTCAGACCGGAGCAATCCAGGTCGGTTTCTA
C. c._NC_002778                 TAGTCCTACGTGATCTGAGTTCAGACCGGAGCAATCCAGGTCGGTTTCTA
C. b. w._E2                     ????????????????????????????????????????????????
C. b. w._E3                     ????????????????????????????????????????????????
C. b. h._E4                     TAGTCCTACGTGATCTGAG??????????????????????????????
C. u._E7                        TAGTCCTACGTGATCTGAGTTCAGACCGG????????????????????
D. N._NC_002784                 CAGTCCTACGTGATCTGAGTTCAGACCGGAGCAATCCAGGTCGGTTTCTA
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