Phylogenetic reconstruction of parental-care systems in the ancestors of birds

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Due to the controversy surrounding incipient avian parental care, ancestral parental care systems were reconstructed in a phylogeny including major extant amniote lineages. Using two different resolutions for the basal avian branches, transitions between the states no care, female care, biparental care and male care were inferred for the most basal branches of the tree. Uniparental female care was inferred for the lineage to birds and crocodiles. Using a phylogeny where ratites and tinamous branch off early and an ordered character-state assumption, a transition to biparental care was inferred for the ancestor of birds. This ancestor could be any organism along the lineage leading from the crocodile–bird split up to modern birds, not necessarily the original bird. We discuss the support for alternative avian phylogenies and the homology in parental care between crocodiles and birds. We suggest that the phylogenetic pattern should be used as a starting point for a more detailed analysis of parental care systems in birds and their relatives.

Keywords: Aves; Amniota; evolution; sex roles; homologous behaviour; alternative phylogenies

1. INTRODUCTION

The ancestral parental care system in birds has raised much interest, not the least since its resolution could help to understand evolutionary routes to various parental care systems in general and in birds in particular. Biparental care is widespread among birds, which might have led to the tacit assumption that this system occurred in the avian ancestor (Lack 1968; Skutch 1976; Emlen & Oring 1977; Silver *et al*. 1985; Clutton-Brock 1991; Krebs & Davies 1993). The question is far from resolved, however, and alternative ancestral-care systems have been suggested. Uniparental male care has been suggested by Van Rhijn (1984, 1990), Elzanowski (1985) and Wesolowski (1994). Van Rhijn mainly builds his argument on the pattern of parental care systems in shore birds (cf. Székely & Reynolds 1995), whereas Elzanowski and Wesolowski to a large extent use palaeontological data as a base for inference. Fossils show that early birds had superprecocial young. To produce superprecocial young with an ability to fly as soon as possible after hatching necessitated the production of huge and costly eggs, and, in turn, male care of eggs evolved as a response to this high-energy cost of egg formation (Elzanowski 1981, 1985; Wesolowski 1994). Wesolowski (1994) also suggests that uniparental male care arose from a state of no postoviposition care (also see Ligon (1999)). Thus, biparental, uniparental male and no care have all been suggested as the ancestral state. Also, female care cannot be excluded from the list of potential ancestral avian-care systems because uniparental female care is common in crocodiles as well as in some presumably early groups of birds, such as waterfowl and gallinaceous birds. For instance, Burley & Johnson (2002)

suggest that biparental care in the ancestor of birds has evolved from a state of limited female care present in the ancestor of all archosaurians.

McKitrick (1992) presented a cladistic analysis of avian relationships, based on various parental care and anatomical character traits. The study inferred biparental care for the avian ancestor, but this result was to a great extent an effect of the assumption that biparental care was the ancestral condition. The outgroups to birds vary in their parental care patterns. For instance, crocodilians are known to have both biparental and uniparental female care (Shine 1988; Coombs 1989), and it is therefore important to include various crocodilian taxa in a phylogenetic analysis. Moreover, phylogenetic reconstruction is more reliable when several outgroups (Maddison *et al*. 1984) and, if possible, fossils (Donoghue *et al*. 1989) are included. Thus, one aim with the present study is to use data for major bird lineages as well as for several outgroups to infer which ancestral-care system was most likely.

Avian relationships are far from resolved and over recent years several alternative phylogenies have been published. Of particular interest when dealing with the avian ancestor are the conflicting phylogenies with regard to the earliest avian branches. Thus, another aim with the present study is to compare the inference concerning ancestral parental care derived from alternative phylogenetic trees.

2. MATERIAL AND METHODS

(a) *Character states*

To be able to compare the behaviour of different groups of animals, in this case various reptilian groups with birds, character traits need to be coded in a way that makes such a comparison possible. For instance, if incubation is used as a character trait (see McKitrick 1992), it follows that it originated within

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the bird clade because it is absent in the outgroups (except for some snake species). In this paper we define parental care as postoviposition care, and nest-building before oviposition is thus not included. However, checking nest-temperature after oviposition, as occurs in some megapodes, belongs to parental care according to this definition. We divide parental care into two major categories, care of eggs and care of young, following the convention of Shine (1988) for reptilians. Such a broad definition of care of eggs includes, for instance, both protection of eggs found in crocodilians and incubation found in birds. Similarly the definition of care of young includes protection, found in both crocodilians and birds, as well as the feeding of young, found only in birds. For each character trait there are four possible states: no care, female care, biparental care, and male care.

Character states were optimized using MacClade v. 3.0 (Maddison & Maddison 1992), with no general assumptions (e.g. Acctran or Deltran) concerning character-trait evolution. However, two alternative assumptions were made with regard to the number of steps involved in various transitions. If a character trait is coded as unordered, this means that each character state can change to any other character state with equal ease. For example, a transition from no care to female care is as easy as one from no care to biparental care or one from uniparental female to uniparental male care. The alternative assumption is that each sex is considered separately in a parental care transition. Thus, a change from female to biparental care requires one step because only the males change in their state of care. Moreover, it takes two steps to change from no care to biparental care, and two steps to change from uniparental female care to uniparental male care, since both of these transitions require a change in each of the sexes. We regard this ordered assumption as more biologically sound than the unordered one (see for instance Gittleman (1981)).

(b) *Outgroups*

We use the phylogeny for Amniota by Gauthier *et al.* (1989) which comprises four extant outgroups to the birds: Mammalia, Chelonia (turtles), Squamata (snakes and lizards) and *Sphenodon* (tuatara) and Crocodylia. In mammals, female care of young is predominant (e.g. Clutton-Brock 1991) and female care of eggs occurs in the monotremes (platypus and echidnas). We have not resolved this group but considered female care to be the ancestral state in mammals.

We have not resolved turtles (Chelonia) but considered no parental care to be ancestral in this lineage. This is so because parental care seems to be totally absent in turtles (Shine 1988). In lizards and snakes maternal care of eggs occurs sparsely in separate groups (reported for 1.3% of lizard species and 2.8% of snake species according to Shine (1988, p. 293)). We follow the conclusion by Shine (1988) that no care is the initial state and that care (by female) has evolved independently several times. Thus, we have not resolved lizards–snakes but considered no parental care to be the state ancestral in this lineage. Tuatara with two extant species, *Sphenodon punctatus* and *Sphenodon guntheri*, form the sister group to lizards–snakes (Gauthier *et al.* 1989). Female tuatara have been found to guard and defend nests with eggs, mainly against conspecific females (Newman 1998).

Crocodilian relationships follow the phylogeny of Brochu (1997) that is based on morphological characters for extant and fossil taxa (fig. 4*a*, p. 491, and fig. 5*a*, p. 492). For three extant taxa included in that phylogeny we did not find any information on parental care behaviour (Chinese alligator, *Alligator sinensis*,

Cuban crocodile, *Crocodylus rhombifer*, and false gavial, *Tomistoma schlegelü*), and these taxa were accordingly excluded from our analysis. An inclusion of these taxa with unknown states would not affect character-trait optimization. Information on parental care behaviours in crocodilians was found in Shine (1988) and Magnusson *et al.* (1989).

(c) *Birds*

Today, the only phylogeny that has attempted to combine a number of species from all avian orders is that of Sibley & Ahlquist (1990). Due to its wide representation of birds we have used genera and species from that phylogeny as a basis for our analyses. Care of eggs and young in birds has been determined using literature listed in Temrin & Sillén-Tullberg (1994) and Temrin & Tullberg (1995).

Certain groups are of special interest in the present study because they are considered to belong to the earliest branches in the avian tree and are therefore of crucial importance for the inference concerning the ancestral branch. Palaeognathae (ratites and tinamous) is placed basal in several phylogenetic studies (Sibley & Ahlquist 1990; McKitrick 1992; Groth & Barrowclough 1999; Van Tuinen *et al.* 2000). Recently, this view was challenged in a study placing Passeriformes as the most basal group, and moreover Galliformes (gallinaceous birds) as a sister group to the palaeognaths (Häarlid *et al.* 1998; Häarlid & Arnason 1999; see also the study by Mindell *et al.* (1999), where a passerine subgroup is placed at the base of the avian tree). Most studies result in gallinaceous birds being the sister group to Anseriformes (waterfowl) and Anseriformes–Galliformes being the sister group to all other birds, together forming the Neognathae (Cracraft & Mindell 1989; McKitrick 1992; Groth & Barrowclough 1999; Van Tuinen *et al.* 2000; but see Ericson *et al.* 2001). As a result of the conflicting phylogenies we have chosen two main resolutions as a basis for reconstructing parental care. One of these, 'passerine basal', places passerines as the basal group and palaeognaths and gallinaceous birds as sister groups. In the other phylogeny, 'palaeognath basal', palaeognaths branch off first and waterfowl–gallinaceous birds is the sister group to all other birds.

The relationships within each tentatively basal group might affect the ancestral branch and it is therefore important to consider alternative phylogenies for these as well. There are several alternative phylogenies for the ratites (Sibley & Ahlquist 1990; Lee *et al.* 1997; Cooper 1997), but all of these place the ostrich, the only species with biparental care, closer to the tip than to the base. Thus, uniparental male care will turn out basal for the palaeognaths in either of these phylogenies, and we have used the one by Lee *et al.* (1997, p. 188) which is based both on molecular and morphological characters. For the waterfowl there are several rigorous phylogenies based on morphological characters (Livezey 1986, 1997), and they confirm the basal placement of Anhimidae, Anseranatidae and Dendrocygnidae, all three groups with biparental care of eggs and young. We have found one alternative phylogeny for gallinaceous birds, which also has a basal position of Cracidae and Odontophoridae (Kornegay *et al.* 1993). The megapodes were not represented in that study.

We have not found alternative passerine phylogenies that include a wide range of taxa. When parental care is reconstructed in the passerine phylogeny of Sibley & Ahlquist (1990), biparental care is inferred for all of the most basal branches, and transitions to uniparental female care occur in some apical branches (see Temrin & Tullberg 1995). Neither have we found

alternative phylogenies that include a wide range of taxa of neognath birds (excluding waterfowl and gallinaceous birds), in this study designated 'other Neognathae'. This group comprises an enormous diversity of forms, e.g. woodpeckers, hummingbirds and rails, shorebirds, birds of prey and penguins. When parental care is reconstructed for this huge group (with the passerines included or not) using the phylogeny of Sibley & Ahlquist (1990), transitions in parental care modes occur in apical branches, and biparental care of both eggs and young is dominating and inferred for the basal branches (see Temrin & Sillén-Tullberg 1994; Temrin & Tullberg 1995). In the present study we only account for the inferred basal state in neognaths and passerines, respectively.

3. RESULTS

When the two parental care characters are optimized over the phylogeny which includes 48 taxa, there are altogether 17–18 transitions in care of young and 10–11 transitions in care of eggs, in either of the two alternative phylogenies. The lowest and highest numbers in these ranges depend on whether the character states were unordered or ordered, respectively.

Care of young is the more transient character trait, but to find out whether this is a general pattern in birds a larger sample of taxa needs to be analysed.

In order to facilitate a description of our results, we pooled the two characters and simply called the ensuing character trait 'parental care'. This character trait denotes whether both or only one of the parents are at all involved with taking care of eggs or young, and the character trait largely corresponds to the care of young. This is because when the female is brooding the eggs and both parents take care of the hatchlings, which is the case in several taxa, the taxa will be coded as having biparental care.

(a) Passerine basal

If passerines constitute the earliest avian clade the result concerning ancestral parental care is unambiguous. Female care is inferred for the archosaurian ancestor (birds and crocodiles) and a transition from female to biparental care is then inferred for the ancestor of all extant birds (figure 1). The result is the same for the unordered and ordered character-trait assumptions.

(b) Palaeognath basal

If palaeognaths constitute the earliest avian clade the results differ between the two assumptions about character transformation (figure 2). If the character trait is regarded as unordered, the inferred state for the crocodile–bird ancestor is female care, whereas the state of the bird ancestor is equivocal with either female, biparental or male care (figure 2a). If, however, parental care is regarded as an ordered character trait, according to our description in § 2a, this ambiguity is resolved. Female care is still inferred for the crocodile–bird ancestor and then biparental care is inferred for the avian ancestor (figure 2b).

4. DISCUSSION

Our analysis resulted in a predominance for female parental care in the ancestral amniote lineages. One unam-

biguous result is that whatever parental care system that was present in the ancestor of birds, it should be a system derived from female care. This result is independent of which phylogenetic hypothesis about avian relationships is used. It is important to keep in mind that the ancestor of birds could theoretically be any creature, for instance a theropod dinosaur, along the lineage leading from the crocodile–bird split up to modern birds (figures 1 and 2). The inferred parental care system for the ancestor of birds is partly dependent on the assumptions concerning transformation between care systems, and in the following we have evaluated these assumptions. However, first we evaluated the alternative phylogenies that we used.

Cytochrome *b* data supported the placement of passerines as the basal avian lineage in a study investigating relationships among a subset of avian orders (Häarlid *et al.* 1998). A second molecular-based study also placed some passerines as the basal avian group, but the passerines themselves were paraphyletic on that tree. A basal position for the ratites could not be excluded when more taxa were added to this analysis (Mindell *et al.* 1999). When nuclear and mitochondrial data were combined for species from all modern avian orders ($n = 24$), a topology in which the palaeognaths were basal, the waterfowl and gallinaceous birds were sister groups, and the neognaths were monophyletic (see figure 2) was well supported (Van Tuinen *et al.* 2000).

Thus, on the basis of these recent studies we find 'palaeognath basal' as the best-supported phylogenetic hypothesis. However, when using an unordered assumption about character-trait transition this phylogeny gives equivocal states for the ancestor of birds. Thus, we must ask whether the two alternative assumptions concerning character-trait transitions are equally robust. We hold that they are not and that it seems unlikely, for instance, that a state of absence of care evolves directly to biparental care, but more probable that the route is taken via uniparental male or female care. Similarly, one might not expect male care to evolve directly into female care (or vice versa) without first passing through a stage with biparental care. This transition scenario is supported in comparative studies of fish (Gittleman 1981; Gross & Sargent 1985; Goodwin *et al.* 1998). In a study on shore birds Székely & Reynolds (1995) found as many transitions from pure or mostly male care directly to pure or mostly female as to full biparental care. However, if parental care is recoded so that all cases where both sexes are involved, albeit to an unequal degree, are coded as biparental, there are no transitions directly between male and female care but always between either of these two states and biparental care. In conclusion, we find that the ordered transition scheme for parental care has more theoretical and empirical support than the unordered scheme in which all transitions between care states are equally possible.

Given the 'palaeognath basal' phylogeny and the ordered transition scheme, we infer female care in the archosaurian and biparental care in the ancestor of birds. Our analysis does not support a transition to uniparental male care in this lineage (e.g. Van Rhijn 1984, 1990; Elzanowski 1985; Wesolowski 1994; Ligon 1999), whether this should be derived from biparental or no care. Our analysis does give support to the idea that parental care as such is homologous for birds and crocodiles.
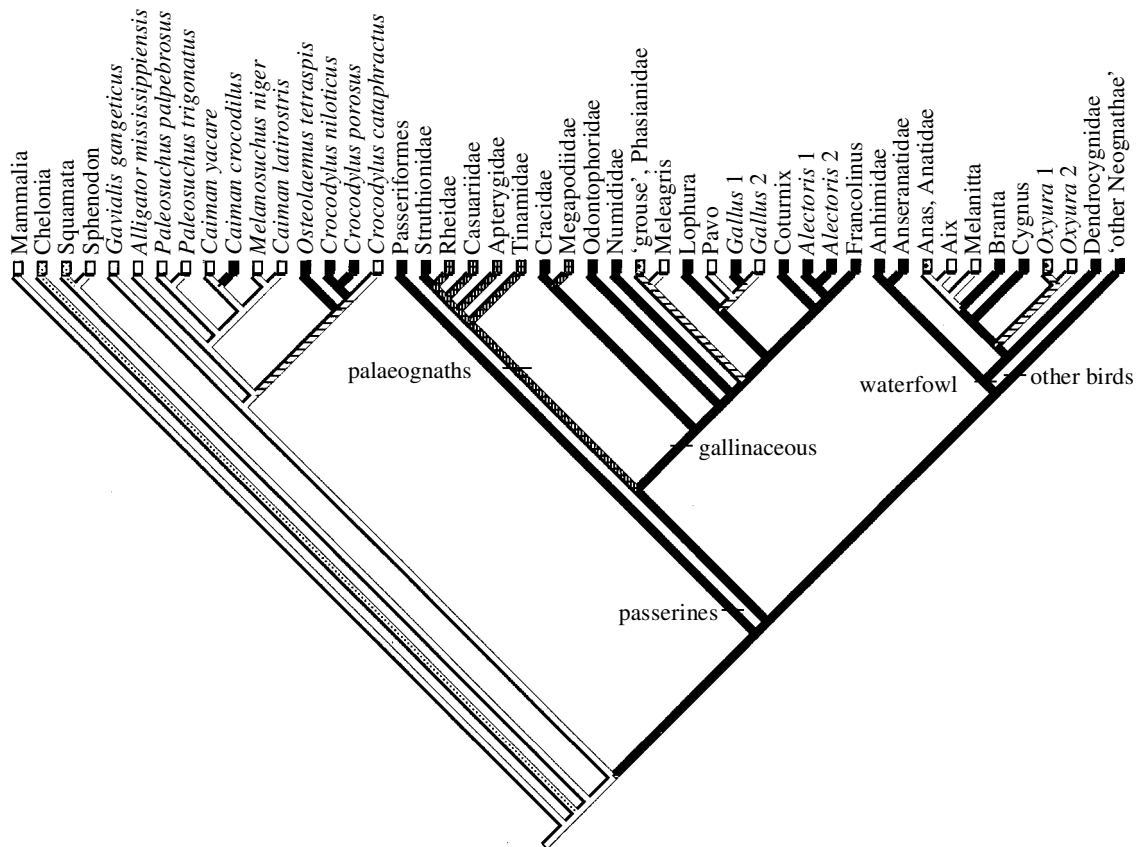
Figure 1. Reconstruction of parental care in a phylogeny where Passeriformes is the most basal avian clade (Häarlid *et al.* 1998) (17 steps). For other avian relationships, see § 2c. The relationship between birds, crocodiles, snakes and lizards (Squamata), tuatara (Sphenodon), turtles (Chelonia), and mammals follow Gauthier *et al.* (1989). Crocodilian relationships follow Brochu (1997). The avian phylogeny includes taxa from Sibley & Ahlquist (1990). Character states are given for each taxon. For illustration purposes, separate genera are shown only for the families with variation in parental care characters. When only family names are given all genera in that family have been included in the original analysis except for the following families (included genera in parenthesis): Tinamidae (*Nothoprocta*, *Crypturellus*), Cracidae (*Penelope*, *Pipile*, *Crax*), Megapodiidae (*Alectura*), Numididae (*Numida*), Dendrocygnidae (*Dendrocygna*). *Gallus* 1 = *G. varius*, *Gallus* 2 = *G. gallus* and *G. lafayetii*. *Alectoris* 1 = *A. graeca*, *Alectoris* 2 = *A. barbara*, *A. rufa* and *A. chukar*. *Oxyura* 1 = *O. jamaicensis*, *Oxyura* 2 = *O. australis* and *O. maccoa*. For further information concerning taxa and sources see Temrin & Tullberg (1994, 1995). Two different assumptions concerning character transformation (see § 2a) produced the same result. A transition from female to biparental care is inferred for the ancestor of birds. Dotted lines, no care; white lines, female; black lines, female and male; checked lines, male; large-dotted boxes, polymorphic; hatched lines, equivocal.

Wesolowski (1994) recognized that two separate origins of parental care in these groups must be assumed if uniparental male care was the ancestral avian condition. He discussed the likelihood of parental care being homologous for birds and crocodiles, and concluded that it is low because such a long time has passed since the split of the two lineages.

The strongest proponents of homology in parental care are found within the field of palaeontology. Although there are problems with inferring behaviour from fossils, some dinosaur fossils are regarded as strong evidence of parental care. Findings of nests with eggs and young in various associations with adults are widely regarded as evidence of parental care in several dinosaur lineages (Coombs 1982, 1989; Horner 1984; Norell *et al.* 1995; Varricchio *et al.* 1997). These findings have been regarded as an indication that parental attendance of eggs may be primitive for dinosaurs, that brooding behaviour evolved before the avian clade (Norell *et al.* 1995) and that postoviposition care is homologous for Archosauria (Coombs 1989; Varricchio *et*

al. 1997). A long time, perhaps 260 million years (Norman 1985), has passed since the split between crocodilians and birds. Crocodiles seem to be a conservative group with very little morphological change in 200 million years, but undoubtedly a lot of cladogenesis has taken place in the lineage leading to the first bird at least 150 million years ago (*Archaeopteryx*). We agree with some of the palaeontologists in so far as the presence of parental care in some of these lineages, as well as similarities between crocodiles and dinosaurs in related characters such as nest structure and egg morphology (Coombs 1989), make homology in parental care between extant birds and crocodiles more plausible.

Which sex was involved in parental care in dinosaurs? This question is hard to answer because there is no information as yet of the sex of, for instance, the individuals of the theropods *Troodon* and *Oviraptor* found in likely brooding positions (Norell *et al.* 1995; Varricchio *et al.* 1997). Varricchio *et al.* (1997) report that the 22 eggs in one *Troodon* nest show a paired arrangement, which,
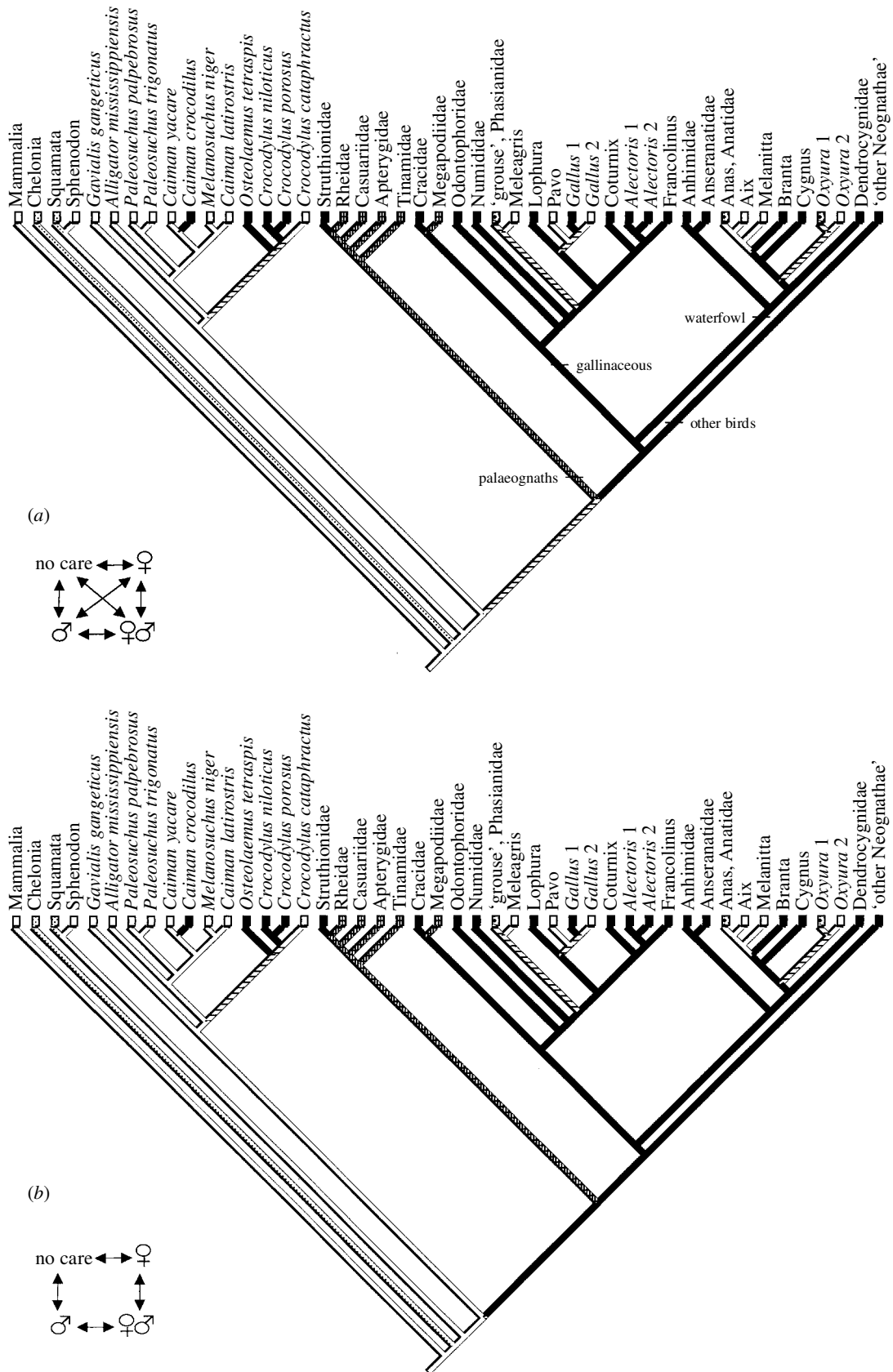
Figure 2. Reconstruction of parental care in a phylogeny where palaeognaths constitute the most basal avian clade (e.g. Van Tuinen 2000). For other avian relationships, see § 2c. Other relationships as in figure 1. Nomenclature and taxa as in figure 1. (*a*) Character unordered. The inferred state for the ancestor of birds is equivocal: either female, male or biparental care. (*b*) Character ordered so that a change of state in one sex is counted as one step (e.g. it takes two steps between no care and biparental care and between uniparental male and female care). A transition from female to biparental care is inferred for the ancestor of birds. Dotted lines, no care; white lines, female; black lines, female and male; checked lines, male; large-dotted boxes, polymorphic; hatched lines, equivocal.

together with egg size, indicates that two eggs were produced at daily or greater intervals (two functional ovaries compared with one in birds). If brooding and an extended egg-laying period indicate a long pair bond between mates as suggested by Varricchio *et al.* (1997), biparental care might indeed have preceded the split between birds and other dinosaurs. Coombs (1989) finds it likely with male assisting the female in guarding nests and providing care to young, but regards the caring sex(es) as an open question because all types of care systems are present in extant archosaurs.

We have carried out a formal cladistic analysis of parental care systems in order to be able to make an inference for the avian ancestor. It is important to note that whatever state is thought to be likely for the ancestor of birds, it requires an account for other close branches. Using the phylogeny that we regard to have the best support, together with a given assumption about the number of steps involved in various character-trait transitions, we infer that female care is homologous for the bird and crocodile ancestor and that biparental care evolved in the ancestor of birds. Fossils indicating parental care in some of the dinosaurs that are related to birds support this solution. We believe that a historical analysis like this limits the number of potential scenarios and we suggest that it be used as a starting point for a more detailed analysis of mating systems in birds and their relatives. For instance, the detailed model described by Burley & Johnson (2002) is compatible with the phylogenetic pattern outlined in our study.

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