

# Evolutionary transitions in parental care in cichlid fish

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Cichlid fishes (Cichlidae) are well suited for testing theories of the evolution of vertebrate parental care. These freshwater teleost fish provide parental care for their offspring, display many different forms of care and have interspecific variation in which sex stays with the young. Here, we assemble the first family-wide composite phylogeny based on morphological and molecular studies, and trace two sets of character evolution: form of care (substrate guarding and mouthbrooding), and sex of care-giver (biparental, female-only, and male-only). Mouthbrooding has evolved from ancestral substrate guarding with 10–14 transitions and 0–3 reversals. The data support hypothesized transitions in the sex of care-giver, with uniparental female care having arisen from biparental care 21–30 times with 0–10 reversals. There is also evidence that male-only care evolved once from biparental care. These transitions in parental care characters are the most numerous reported for any family of vertebrates and, to our knowledge, provide the first quantitative support for models of parental care evolution in fish.

**Keywords:** Cichlidae; evolution; phylogeny; reproduction; sexual selection; teleost

## 1. INTRODUCTION

Advances in our understanding of the evolution of parental care have come from two approaches: cost–benefit analyses of behaviour by contemporary species, and reconstruction of historical changes in patterns shown by different taxa. The former approach examines fitness benefits relative to costs to both sexes, as well as conflicts and cooperation between the sexes (see Clutton-Brock 1991). These trade-offs have been used to infer the probable directions of evolutionary transitions in parental roles (Maynard Smith 1977; Baylis 1981; Gross & Sargent 1985; Balshine-Earn & Earn 1998). However, measurements of costs and benefits in extant species do not examine directly the past transitions in care that have led to the diversity seen today. Historical reconstruction of evolutionary events allows estimation of transitions in the form of care and the sex of care-giver, and can test theories predicting coevolution and constraints upon characters and biases in directions of change (Brooks & McLennan 1991; Harvey & Pagel 1991; Székely & Reynolds 1995; Temrin & Tullberg 1995). Our study uses this historical approach to investigate transitions for cichlid fish (Cichlidae).

Of the 422 families of teleost (bony) fish, 87 (21%) show some form of post-fertilization care of eggs; of these, male-only care is found in 49%, care by females in 7% and biparental care in 13% of families, whereas the remaining 31% include more than one of these categories (Blumer 1979, 1982; Gittleman 1981; Gross & Sargent 1985). Cichlid fish (*ca.* 195 genera and more than 1300 species) provide the best opportunity for the study of evolution of care in teleosts

because they show diverse forms of parental care (substrate guarding and delayed and immediate mouthbrooding) and variation in which sex provides care (biparental, female-only and male-only care) (Blumer 1982; Keenleyside 1991*b*). Furthermore, extensive ecological, behavioural and phylogenetic information is available for this family, which has led to considerable speculation about the evolution of various forms of parental care.

Substrate guarding (care of eggs and larvae in a crevice or nest) by both parents is widely considered to be the ancestral care state in cichlids (Lowe-McConnell 1959; Iles & Holden 1969; Peters & Berns 1982). The evolution of mouthbrooding, perhaps to increase mobility during parental care, has been accompanied by desertion by males. Biparental care of offspring is traditionally considered ancestral to uniparental (female or male) care (see Keenleyside 1991*b*). To date, these hypotheses and others, based on morphology and biogeographic information, have not been tested within a comprehensive phylogenetic framework. Our study uses this approach by tracing discrete care characters onto a composite phylogeny for the family. We show that the number of transitions in the form of care has previously been underestimated, and we present the first estimates for evolutionary transitions in sex of the carer. These findings are used for general inferences about stability and bias in the evolution of parental care.

## 2. MATERIALS AND METHODS

### (a) *Phylogenetic tree reconstruction*

A composite phylogeny was assembled for the family Cichlidae, described as monophyletic by Strelman & Karl

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(1997). Phylogenetic data remain inconclusive about the outgroup to the Cichlidae (Streelman & Karl 1997). Stiassny (1991) provided the initial relationships between the main sub-groupings of genera and established the monophyletic status of Neotropical and African clades. Relationships among New World cichlids were provided by Casciotta & Arratia (1993) and Stiassny (1991). The Madagascan genus *Oxylapia* was positioned by P. Reinthal (personal communication). We used Greenwood (1985), Stiassny (1991) and van der Bank (1994) for West African genera. All other major African taxa were placed according to Greenwood (1983a) and Nishida (1997). Phylogenies for tilapiine and lamprologine genera were inserted at positions suggested by Sodsuk (1993) and Schliewen *et al.* (1994), and Sturmbauer *et al.* (1994), respectively. Meyer *et al.* (1990) established the monophyletic status of the Lake Malawi and Victoria clade, placing Lake Tanganyikan cichlids as ancestral. Relationships within Lakes Malawi and Victoria were not required, because there were no transitions in 'care form' or 'sex of carer' in these clades.

When more than one phylogeny was available for a clade (e.g. Lake Tanganyika), we present those that included the most genera and with the best resolution. However, we also considered alternative trees in the analyses. The composite tree presented should not be considered a definitive phylogeny; it will certainly change as more data become available. Because none of the phylogenies was based originally upon reproductive characters, any errors will be random with respect to direction of transitions among forms of care, and the sex of the care-giver. The composite phylogeny includes 174 genera, which is 89% of the total for the family, thereby providing a representative taxonomic spread.

### (b) *Reproductive data*

Reproductive data were extracted from key texts (Trewavas 1983; Loiselle 1985; Richter 1989; Keenleyside 1991a; Kawanabe *et al.* 1997; Kuwamura 1997; Stawikowski & Werner 1998). These were supplemented with additional primary literature and original descriptions. Reproductive information on either form of care or sex of care-giver was missing for four genera but these genera were included in the tree for completeness. We considered form of care (substrate guarding and mouthbrooding), and the sex of the care-giver (biparental, female-only and male-only). The two forms of mouthbrooding—delayed (beginning when eggs hatch) and immediate (beginning at spawning)—were combined because the literature often failed to distinguish between them consistently. Where data for both forms of mouthbrooding were available we found no change in overall patterns. We defined 'biparental' as any species where the male and female both participated in some form of behaviour likely to increase the fitness of their offspring (care of eggs, juveniles or defence of nest) (see also Keenleyside 1991a).

### (c) *Analysis of character evolution*

The composite phylogeny was assembled in MacClade 3.07 (Maddison & Maddison 1992). Multiple nodes were treated as unresolved 'soft polytomies', rather than multiple speciation events. We used unordered character states, allowing any form of care or sex of care-giver to transform into any other using the Fitch parsimony option (Maddison & Maddison 1992). Where reproductive data are not shown on the tree tips, the program assigns the most parsimonious reproductive character to the branch. The minimum and maximum numbers of transitions in character states were calculated by hand because the tree included equivocal branches.

Alternative phylogenies were used to compare results from the composite phylogeny. Alternative trees were available for the Neotropical cichlids (Stiassny 1991), West Africa (Greenwood 1983b), the tribe Tilapiini (Sodsuk & McAndrew 1991; Pouyaud & Agnese 1995), and the East African and riverine groups (Nishida 1991; Kocher *et al.* 1993, 1995; Sturmbauer & Meyer 1993; Streelman & Karl 1997; Mayer *et al.* 1998).

## 3. RESULTS

### (a) *Transitions between substrate guarding and mouthbrooding*

The most parsimonious reconstruction of the evolution of form of parental care in cichlids had a minimum of 13 steps (figure 1). This phylogeny shows that substrate guarding is the ancestral state within the family, and mouthbrooding is the most common form of care (figure 2a). The tree shows that mouthbrooding has evolved from ancestral substrate guarding 10–14 times (figure 3a). This includes 6–7 cases in New World clades and 4–7 cases in African clades. There is evidence for only 0–3 transitions in the reverse direction, including one possible case in New World genera and two in African genera.

The transitions in form of care have occurred at different taxonomic levels (table 1). Although it remains to be seen whether this reflects the timing of events. A strong geographical dichotomy is shown in forms of cichlid care. There are 117 mouthbrooding genera, of which 94% occur in African clades, and of the 60 substrate-guarding genera, 70% occur in the New World clades (figure 2a). The Lake Victoria and Lake Malawi clade account for 59 (54%) of the African mouthbrooding genera (figure 1; labelled A).

### (b) *Transitions between biparental and uniparental care*

The most parsimonious reconstruction of the evolution of biparental and uniparental care reveals a minimum of 29 evolutionary steps (figure 4). This phylogeny shows that biparental care is ancestral in cichlids and that uniparental care is most common overall (figure 2a). There is evidence that female care has evolved from biparental care 21–30 times, with 0–10 reversals (figure 3b). In addition, male care has evolved independently, once from biparental care with no reversals. In total, uniparental care (by either sex) evolved from biparental care 7–9 times in the New World clades and 14–21 times in the African clades. Biparental care may have evolved from uniparental care 0–10 times in the African clade.

The transitions between sex of care-giver occur evenly at different taxonomic levels within the tree (table 1). Of the 174 cichlid genera presented, 109 (63%) are uniparental carers, with all but one providing female-only care (figure 4). Only two species in the polyphyletic genus *Sarotherodon* are known to provide male-only care (figure 4). Fifty-nine (55%) of the female caring genera occur in Lakes Malawi and Victoria (figure 4). Biparental care is conserved in the New World clade with only one-third of the transitions to female care having occurred there.

Of the 117 mouthbrooding genera for which data on sex of carer were available, 95 (81%) genera show uniparental mouthbrooding compared with only 25 (21%) that show biparental mouthbrooding (figure 2b).

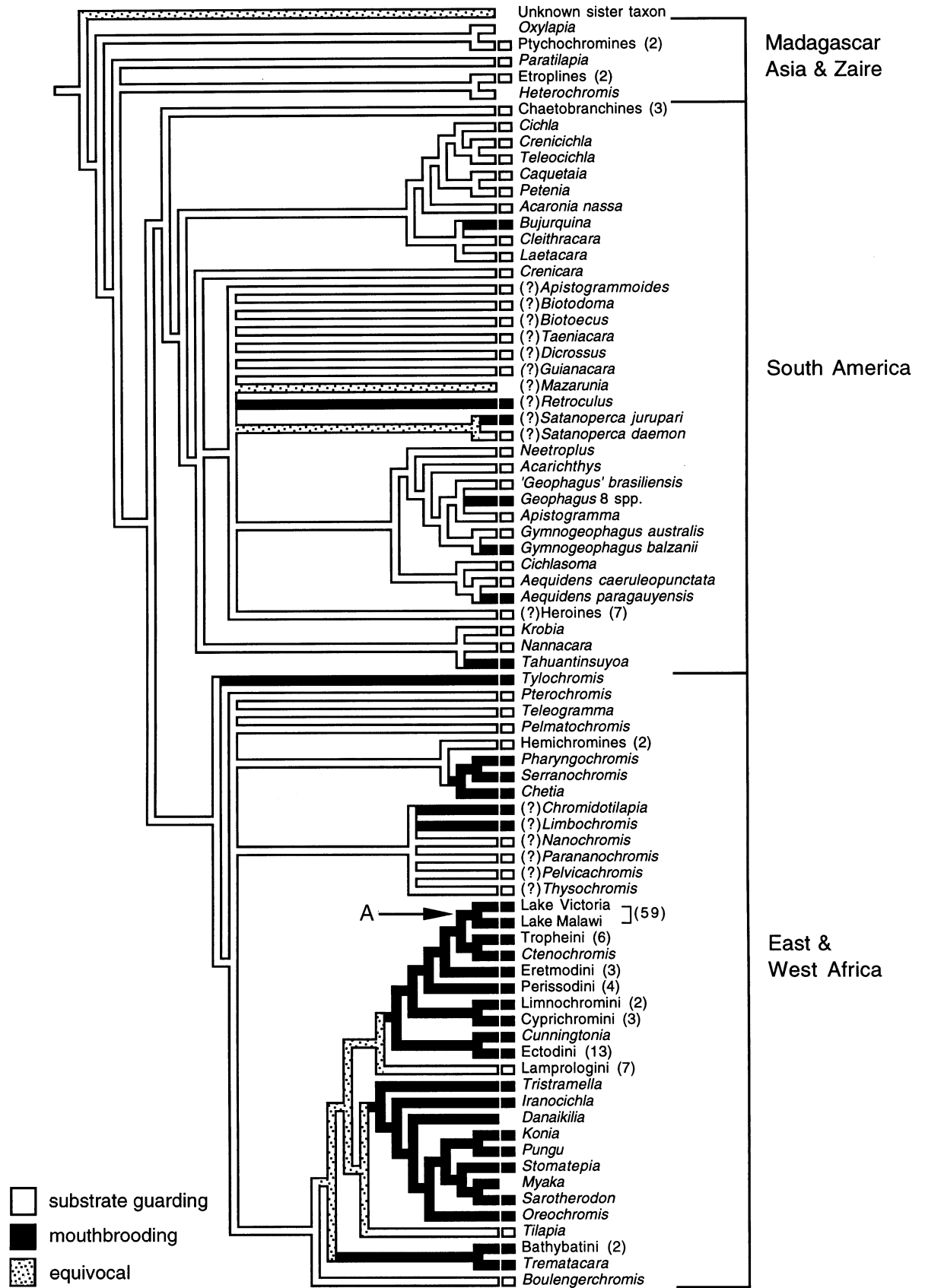


Figure 1. Phylogenetic distribution of the forms of care given to eggs and/or juveniles in the family Cichlidae. Numbers in parentheses show the number of genera in the group. Taxa with (?) placed before them indicate a poor knowledge of phylogenetic relationships. Boxes next to taxa indicate that reproductive data were available. 'A' indicates the clade that accounts for 55% of African mouthbrooding genera.

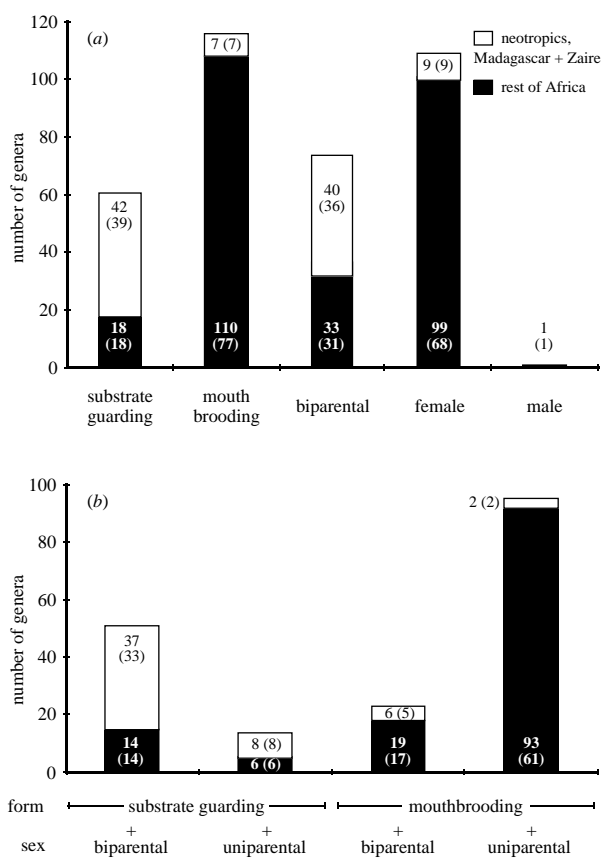


Figure 2. (a) Numbers of cichlid genera providing different forms of care and sex of care-giver ( $n=173$  genera). (b) Numbers of cichlid genera combining both the form of care and sex of the care-giver ( $n=170$  genera). Shading of the bars indicates the major biogeographic groupings of genera from the major clades, ancestral genera from Madagascar, Asia and Zaire, and the sister clades from South America and Africa. Numbers in the bars indicate the number of genera extrapolated from the available data given in parentheses. Taxa where branch tracings could not be assigned a character were not included in this analysis.

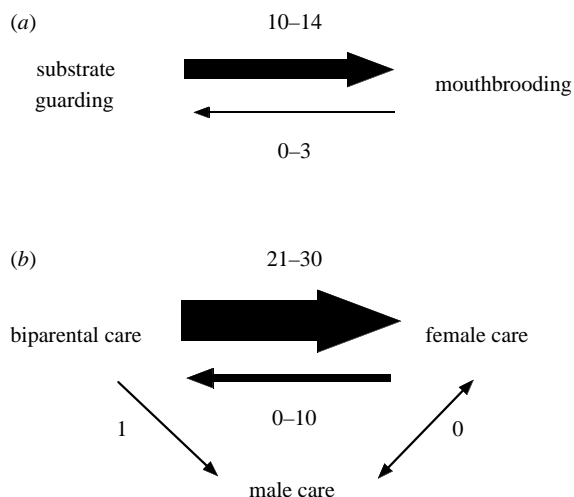


Figure 3. Transitions between (a) substrate guarding and mouthbrooding, and (b) biparental, female-only and male-only care. Arrow widths are proportional to the number of transitions.

However, the phylogeny shows that a single transition to female care accounts for 67 (57%) mouthbrooding genera (figure 4; labelled A).

#### (c) *Alternative trees for comparison*

Most of the alternative phylogenetic hypotheses supported the major patterns described above (table 2). Seven of the ten available alternative phylogenies did not affect our estimates of transitions between substrate guarding and mouthbrooding. Four alternatives had no effect on transitions in sex of care-giver, whereas four reduced slightly the number of minimum transitions from biparental to female care (table 2). The only substantial change was the placing of *Eretmodini* and *Perisodini* (Kocher *et al.* 1995), which resolved the equivocal East African lake clades (figure 4; labelled B), and supported two reversals from mouthbrooding to substrate guarding and five reversals from female to biparental care.

## 4. DISCUSSION

### (a) *Evolution of form of parental care*

Our results support the hypothesis that substrate guarding is the ancestral mode of care and mouthbrooding is derived within the Cichlidae (Lowe-McConnell 1959; Peters & Berns 1982; Keenleyside 1991b). We found mouthbrooding has arisen 10–14 times from ancestral biparental substrate guarders. This increases the estimate of 3–7 transitions identified by McLennan (1994) based on the phylogeny of Stiassny (1991), and supports the author's prediction that more transitions would be identified as the phylogeny became better resolved.

Keenleyside (1991b) noted numerous morphological and behavioural adaptations associated with forms of cichlid care. Research suggests that the evolution of the following traits have accompanied the evolution of mouthbrooding: loss of adhesive threads on eggs (Peters & Berns 1982), reduced fecundity, and increased egg size with higher juvenile survival (Noakes & Balon 1982). Oral transport of offspring between excavated pits by substrate guarders could have provided the first step toward the evolution of mouthbrooding, for example if the young were retained in the mouth for some time to avoid predation (Lowe-McConnell 1959; Baylis 1981).

### (b) *Evolution of sex of carer*

Our estimates indicate that, from a biparental ancestor (Lowe-McConnell 1959; Peters & Berns 1982; Keenleyside 1991b), cichlids evolved female care 21–30 times, with a possible 0–10 reversals, and male care evolved once. The sex of the carer has been more evolutionarily labile than has the form of care (30 compared with 13 steps). Changes in the sex giving care were primarily due to reductions in care by males. Reductions in male care have also been shown in shorebirds (Charadriidae) (Székely & Reynolds 1995), and were attributed to possible benefits to males for additional mating opportunities (Reynolds & Székely 1997). Such reversals in cichlids may have occurred in response to shifts in operational sex ratios (Balshine-Earn 1996), food abundance (Townsend & Wootton 1984) or predation intensity (Townsend & Wootton 1985). The division of parental care behaviour between the sexes may predispose

Table 1. *Taxonomic levels of transitions between form of care and sex of care-giver*

(Transition counts show minimum and maximum estimates based on figures 1 and 4.)

	form of care		sex of care-giver	
	substrate guarding to mouthbrooding	mouthbrooding to substrate guarding	biparental to female	female to biparental
within genera	3–4	0–1	7	0–1
between genera	5–6	0	8–13	0–4
between higher clades	2–4	0–2	6–10	0–5
total	10–14	0–3	21–30	0–10

Table 2. *Comparison of transitions with alternative trees, presenting minimum and maximum estimates*

(n.c., no change in estimate because phylogenetic relationships either did not alter the character tracing, or no transitions in characters occurred within the clade.)

study	form of care		sex of care-giver	
	substrate guarding to mouthbrooding	mouthbrooding to substrate guarding	biparental to female	female to biparental
this study	10–14	0–3	21–30	0–10
Greenwood (1983 <i>b</i> )	n.c.	n.c.	21–28	2–10
Kocher <i>et al.</i> (1993)	11–13	0–1	n.c.	n.c.
Kocher <i>et al.</i> (1995)	10–12	2–3	18–24	5–12
Mayer <i>et al.</i> (1998)	10–15	n.c.	17–29	1–14
Nishida (1991)	n.c.	n.c.	n.c.	n.c.
Sodsuk & McAndrew (1991)	n.c.	n.c.	20–30	0–11
Stiassny (1991)	n.c.	n.c.	n.c.	n.c.
Streelman & Karl (1997)	n.c.	n.c.	n.c.	n.c.
Sturbauer & Meyer (1993)	n.c.	n.c.	18–27	2–12

females to remain with the young if males desert. In many biparental cichlids, females perform all brood care activities and maintain closer contact with the eggs and young than males, which mainly defend the territory (Keenleyside 1991*b*).

Gittleman (1981) inferred 21 transitions between the caring sexes in teleost fish, and hypothesized that the direction of parental care was from no care to male-only to biparental to female-only to no care. This was supported by Gross & Sargent's (1985) cost–benefit model. Our evidence supports one pathway in this cycle, the transition from biparental to female-only care in Cichlidae. Surprisingly, an additional pathway to those described above was identified in the tilapiines with male care evolving from female care, according to the phylogeny of Pouyaud & Agnese (1995). There is insufficient evidence to say whether a transition occurred from female to male care directly or by means of an extinct or unknown biparental ancestor. Similar apparent direct transitions from predominantly male to female care have been shown in shorebirds in the genus *Calidris* (Székely & Reynolds 1995).

### (c) *Coevolution of parental care characters*

Evidence for the coevolution of parental care characters has yet to be explored in teleost fish. Our analysis shows that uniparental mouthbrooders evolved

from biparental substrate guarders and mouthbrooders as hypothesized by Iles & Holden (1969), and female-only and biparental mouthbrooding evolved independently from biparental substrate guarding as proposed by Lowe-McConnell (1959) and Kraft & Peters (1963). Transitions between biparental and female-only care do not appear to be biased by the ancestral condition of substrate guarding or mouthbrooding, with transitions in the substrate guarding Lamprologini (4–6 times) being similar to its sister mouthbrooding clade (4–7 times).

From the evidence in this study, cichlid fish join anurans (Beck 1998), reptiles (Shine 1985), shorebirds (Székely & Reynolds 1995) and elasmobranch fish (Dulvy & Reynolds 1997), as highly labile taxa in forms of parental input. There is considerable diversity among these taxa in the kinds of care provided, including incubation (birds), live-bearing (some reptiles and elasmobranchs), and offspring guarding and transport (some anurans and teleost fish). Future studies of the life histories, sexual behaviour and ecology of these taxa should help determine any common causes of these diverse forms of parental care.

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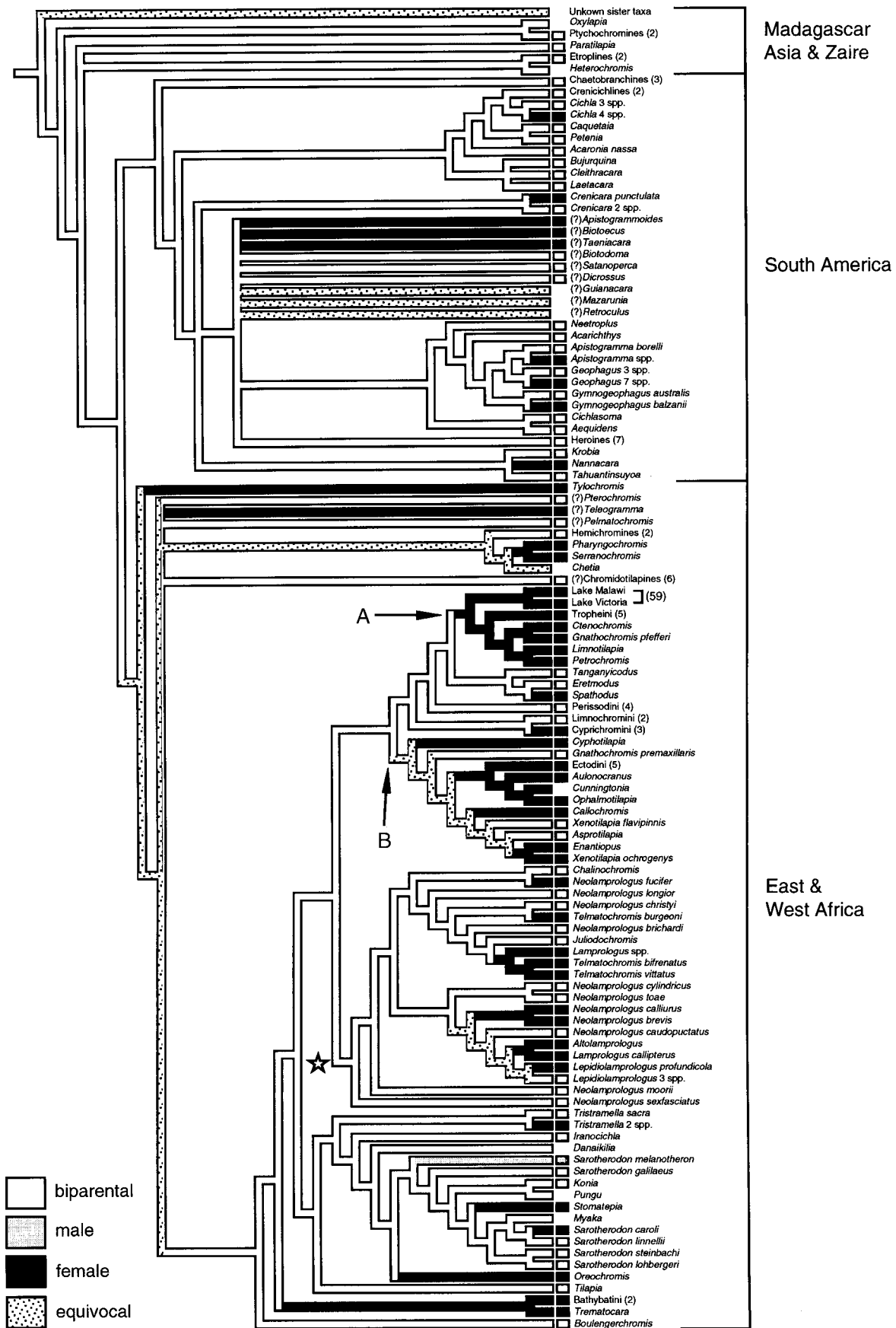


Figure 4. Phylogenetic distribution of the sex of the care-givers to eggs and/or young in the family Cichlidae. Numbers in parentheses show the number of genera in the group. Taxa with (?) placed before them indicate a poor knowledge of phylogenetic relationships. Boxes next to taxa indicate that reproductive data were available. 'A' indicates a single transition to female care that accounts for 57% of mouthbrooding genera. 'B' indicates the equivocal clade that is resolved by the alternative positioning of the tribe Eretmodini, sister to the Lamprologini (marked with a star) (Kocher *et al.* 1995).

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