markedly so. Thus, the Tumbiana stromatolite assemblage is noteworthy more for its age than for its aspect.

Most remarkable, however, is the fact that the metabolic capabilities of the constructing microorganisms can be determined. As the stromatolites accreted in evaporative lakes that occupied interior drainage basins on a basaltic plateau, essentially isolated ecosystems with negligible surficial inputs of energy and nutrients, heterotrophic metabolism of allochthonous organic nutrients cannot have been the basis of the local trophic hierarchy. The scarcity of sedimentary iron and sulfur mineralization indicates that volcanic and hydrothermal discharges into the Tumbiana lakes were minimal, so obligate consumers of juvenile hydrogen, hydrocarbons, or reduced sulfur must have been scarce. The sulfate deficit requires that anaerobic photosynthesis was insignificant. This leaves oxygenic photosynthesis as the only metabolic process capable of accounting for the abundance of biogenic material in the lakes. Given the equivocal nature of other data (*1*), the Tumbiana stromatolites thus constitute perhaps the firmest evidence of an Archaean trophic system based upon such metabolism.

Carbon isotope data (*11, 18, 19*) suggest both eubacteria and archaebacteria inhabited the Tumbiana lakes. Exceptionally light organic carbon (−40 to −50 per mil) associated with rather light carbonate carbon (0 to −4 per mil) implies that archaebacterial methanogens recycled carbon previously fixed by eubacterial photosynthesizers, the resulting methane being then consumed by methylotrophs (*20*). The isotopic differences between late Archaean lacustrine and marine kerogens (*18*) indicate that sulfate reducers had also evolved, largely excluding methanogens from oceanic environments by consuming most of the available organic substrate. Thus, the late Archaean biota had perhaps reached the maximum level of metabolic complexity and diversity possible in a suboxic world inhabited exclusively by prokaryotes. A period of evolutionary stasis apparently then ensued for about a billion years until the advent of eukaryosis (*21*) and a well-oxygenated atmosphere (*22*) in the latter part of the early Proterozoic.

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Interspecific Brood Parasitism in Blackbirds (Icterinae): A Phylogenetic Perspective

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An 852–base pair region of the cytochrome-b gene was sequenced for the brood parasitic cowbirds and 20 additional taxa of the New World blackbirds (Icterinae). The goal of the study was to determine (i) whether interspecific brood parasitism is multiply derived within the assemblage and (ii) the nature of the evolutionary transformation between various forms of interspecific brood parasitism. Cladistic analysis of the sequence data indicates that brood parasitism evolved a single time within the Icterinae. The primitive form of interspecific brood parasitism in this assemblage is host-specificity, with host-generality representing the derived condition.

AVIAN INTERSPECIFIC BROOD PARASITISM (INTER), the laying of eggs by an individual of one species in nests of other species with subsequent care for the parasite young provided by the hosts, has been the subject of much interest over the past century (*1–3*). Most recently, avian brood parasitism has been proposed as an ideal system for the study of coevolution (*3*). However, studies of the evolution of this life history strategy have been hindered by the lack of explicit historical frameworks in the form of well-substantiated phylogenies for the taxa involved (*4*). Although a phylogeny does not necessarily fully resolve the sequence of events in the evolution of INTER, it does make possible the elimination of some alternative hypotheses (*6*).

Different species of avian brood parasites use from one to as many as 240 host species. Is this broad range of INTER connected by a simple evolutionary trajectory, and if so, does one extreme or the other represent the apomorphic condition? Theoretical investigations of parasite-host coevolution (*3, 7*) suggest that as hosts develop defense mechanisms, brood-parasitic species may evolve in one of two ways: brood parasites may parasitize progressively fewer species over time as they develop responses to host defenses or, if naïve potential hosts are available, brood-parasitic species may alter their host selection. The former process could be characterized as an evolutionary transformation from host generalist to host specialist, whereas the latter could be characterized as maintenance of host number through time or perhaps a shift toward increasing generalization in host selection. A phylogeny for a group of birds that includes species that are specialized, intermediate, and generalized with respect to their selection of hosts provides a test of these predictions. If use of many host species is the initial stage in the evolution of INTER (*5*), then specialized species should form a monophyletic clade. Conversely, if use of one or a few host species is the primitive condition of INTER, then species parasitizing many host species should form a monophyletic clade. In either case, species parasitizing intermediate num-

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bers of host species should form the sister taxon of the clade with the derived condition. If both processes are occurring within an assemblage, then neither specialists nor generalists would be expected to form monophyletic clades.

The cowbirds (Passeriformes: Emberizidae: Icterinae) provide an opportunity to examine these hypotheses from a phylogenetic perspective. The six cowbird species exhibit the required variety in host specificity (*1*): *Molothrus badius* is a nest parasite (it takes over nest of other species) but rears its own young; *M. rufoaxillaris* is a host specialist parasitizing a single species (*M. badius*); two species (*M. aeneus* and *Scaphidura oryzivora*) are intermediate, parasitizing primarily one or two confamilial genera; two species (*M. ater* and *M. bonariensis*) are generalists, parasitizing a wide assortment of species (*8*). In order to avoid problems of circularity, phylogenies used to test evolutionary hypotheses must be generated with characters other than those about which the evolutionary hypotheses make predictions (*6*). The data for this study consisted of DNA sequences of the mitochondrial cytochrome-b gene, obtained by polymerase chain reaction (PCR) (*9*) and dideoxy DNA sequencing (*10*). Examined were 852 base pairs for the six cowbird species, 20 additional blackbird species (representing an additional 16 genera), and two species from related passerine families (*11*).

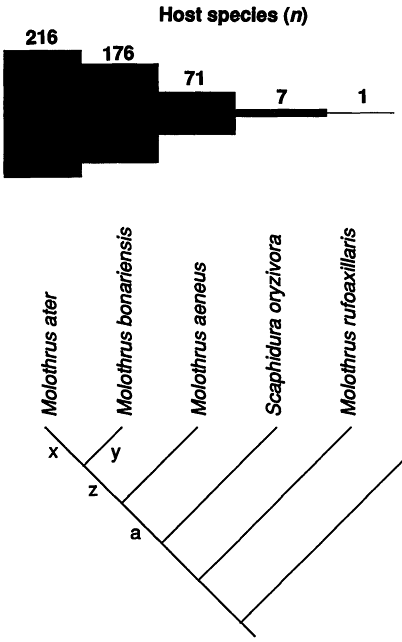

Fig. 1. Phylogeny of the brood-parasitic cowbirds. A single most parsimonious tree [length, 46; consistency index (excluding uninformative characters), 0.717] was obtained. Numbers of host species reported for each of these brood parasites (*20*) are presented above the phylogeny. A trend from host specialist to host generalist is strongly indicated. Linkage of the outgroup at branches x, y, or z rather than as shown would result in trees of length 58, 60, and 55, respectively. The genus *Molothrus*, as currently described, is clearly not monophyletic owing to the placement of *Scaphidura* as the sister taxon to a subset of this genus. Recommendations concerning changes in nomenclature will be made elsewhere.

Of the 852 base pairs examined, 247 were potentially informative with respect to relationships among the 26 blackbird taxa. Parsimony analysis of these data (*12*) identified eight equally shortest trees, all of which confirmed that the brood-parasitic cowbirds represent a monophyletic assemblage. The DNA data provide no evidence to support placement of the nonparasitic *M. badius* adjacent to or within this assemblage nor do they argue against such a relationship. Monophyly of the brood-parasitic cowbirds is consistently supported even when randomization methods are applied to the original data (*13, 14*). To investigate relationships within the assemblage of brood parasites, a subsequent analysis was restricted to these taxa using *badius* as the outgroup. Thirty base pairs (5 first position, 1 second position, and 24 third position sites) were potentially informative about relationships within the brood-parasitic cowbirds with respect to *badius* (Table 1). Of these, seven sites had experienced transversions within the ingroup (all at third positions of codons).

An exhaustive search identified a single most parsimonious tree (Fig. 1). Two additional trees were found within five steps (10% longer than the shortest tree) of the most parsimonious tree with consistency indices (excluding uninformative characters) of 0.702 and 0.660. These less parsimonious trees suggest that branch a in Fig. 1 is not as strongly supported by the data as are the remaining internal branches. This is consistent with the observation that all internal branches except branch a are supported by unreversed transversions. Use of other blackbird taxa as the outgroup instead of *badius* had no further effect on tree topology.

The fact that the two generalist taxa form a monophyletic clade with a taxon exhibiting intermediate levels of host-specificity as the sister taxon supports the hypothesis that the generalized form of brood parasitism is the derived condition in cowbirds. A transformation series from nonparasitism, through brood parasitism with host specialization, to brood parasitism with large numbers of host species, is entirely consistent with the cowbird phylogeny presented in Fig. 1. For host generalization to be the primitive condition, the outgroup would have to join the topology in Fig. 1 at branches x, y, or z resulting in increased tree lengths of 12, 14, and 9 steps, respectively.

These results are in conflict with the hypothesis that as hosts develop defense mechanisms against parasitism, parasites should specialize on fewer host species (*3,* 7). As explained by Rothstein (*3*), continued parasitism on these hosts will occur only if the parasite evolves responses to the developing defense mechanisms. Such an "arms race" is hypothesized to preclude use of large numbers of host species and, therefore, host specialization should evolve. Cowbird hosts have clearly evolved defense mechanisms against brood parasitism (*1, 3*), yet host generalization appears to be the derived state in this assemblage. An alternative means of overcoming the problem posed by the evolution of host defense mechanisms is use of additional host species; if available, continued use of hosts with defense mechanisms would be unnecessary. Furthermore, it could be argued that use of many host species would lower the cost of parasitism on any single host and thereby reduce the probability that hosts will develop defense mechanisms (7). Such a scenario is consistent with the pattern of host utilization observed in cowbirds.

If, as these results suggest, host specialization is the initial form of INTER, then it is logical to ask whether intraspecific brood parasitism (INTRA), an extreme form of host specialization, is the precursor to INTER (*2*). However, if true, why is the latter so rare given the apparent ubiquity of the former (*15*)? The relative frequency of IN-

Table 1. Thirty phylogenetically informative characters derived from an 852–base pair fragment of the cytochrome-b gene. Character numbers refer to positions within this fragment. Site 1 corresponds to position 15,032 of the chicken mitochondrial genome (*18*).

Species	Nucleotide position																													
	11	14	43	158	207	218	228	248	347	365	377	401	422	437	476	485	509	605	647	659	674	701	707	759	773	774	776	798	824	833
M. ater	C	A	G	T	G	C	G	T	A	A	C	C	A	C	C	T	C	C	C	C	A	C	T	C	A	G	C	T	A	A
M. bonariensis	C	A	G	T	G	T	G	T	A	C	T	C	A	A	C	T	C	C	C	C	A	C	T	C	A	G	C	T	A	A
M. aeneus	T	A	G	T	A	T	G	T	A	G	T	C	A	A	C	T	C	T	A	C	A	T	C	T	A	G	T	C	G	C
S. oryzivora	C	G	A	C	A	T	A	T	A	G	C	T	A	G	C	C	C	T	A	C	A	T	C	T	A	G	T	C	G	C
M. rufoaxillaris	C	G	G	C	G	T	G	C	C	G	T	T	C	G	A	C	T	T	G	T	T	T	C	C	C	A	T	C	A	C
M. badius	T	G	A	C	G	C	A	C	C	A	C	C	C	G	A	C	T	C	A	T	T	T	C	C	C	A	C	C	A	C

TRA suggests that the conditions that favor parasitism of other species are unlikely to be simple elaborations of the conditions selecting for parasitism of conspecifics.

One line of evidence used to promote this hypothesis has been refuted by the cowbird phylogeny presented herein. Payne (*2*) suggested that INTRA followed by the development of INTER explained the parasite-host relationship between *M. rufoaxillaris* and *M. badius*. However, Payne assumed that these two species were closely related. This assumption now appears invalid.

The apparent distance between *M. rufoaxillaris* and *M. badius* is of added interest in light of their plumage morphologies. Although adult plumages are distinctive (*M. rufoaxillaris* is predominantly black and *M. badius* is predominantly light gray) the nestling plumages are nearly indistinguishable (*1, 16, 17*). Hudson (*16*) and Friedmann (*1*) concluded that this similarity reflected recency of common descent rather than any form of mimicry on the part of the parasite. They supported this argument with the observation that other brood parasites are quite successful at parasitizing hosts morphologically dissimilar from themselves without employing any form of nestling mimicry. However, the results presented herein refute the hypothesis that these two taxa are sister taxa. Even if *M. badius* is the sister taxon to the remaining cowbirds (the current data are uninformative about this question), these results suggest that these two taxa have not shared a common ancestor for a considerable period of time. Therefore, the similarity in nestling plumage patterns, whether due to convergence or parallelism, suggests that there is an advantage derived by *M. rufoaxillaris* as a result of the close resemblance of its young to those of the host species.

The lack of data uniting *M. badius* with the remaining cowbirds has an additional consequence for our understanding of the evolution of INTER. *Molothrus badius* is a nest parasite but rears its own young [a behavior found in many other bird species (*2*)]. If this species is the sister taxon to the parasitic cowbirds as has been assumed on behavioral grounds, then nest parasitism may be the preliminary step in the transformation series from nest building to generalized brood parasitism. Conversely, if any of the other nest-building blackbirds is the true sister taxon of the brood-parasitic cowbirds, then brood parasitism presumably evolved independently of the nest parasitism exhibited by *M. badius*.

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Activation of T Cells by a Tyrosine Kinase Activation Domain in the Cytoplasmic Tail of CD3 ϵ

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The multichain T cell antigen receptor functions by interacting with and activating one or more nonreceptor tyrosine kinases. The cytoplasmic tail of the ζ chain can activate T cells independently of the rest of the receptor complex. The function of the remaining invariant CD3 chains remains unknown. A 22–amino acid region of the cytoplasmic tail of CD3 ϵ was also able to independently activate T cells. Stimulation of T cells by means of the cytoplasmic tails of either ζ or CD3 ϵ resulted in quantitatively distinct patterns of tyrosine phosphorylation, suggesting activation of different biochemical pathways.

THE ABILITY OF ANTIGEN RECEPTORS to transduce signals to multiple biochemical cascades is the central event of immune cell activation. For the T cell antigen receptor (TCR), one or more Tyr kinases likely have a proximal and essential participation in T cell activation (*1*). Exactly how the receptor couples to its activation pathways is not clear. Evidence that the receptor complex associates with the Fyn Tyr kinase suggests that Fyn may be one potential mediator of early biochemical events (*2*). The receptor is an eight-chain transmembrane complex composed of four dimers (*3*). The clonotypic chains (generally α and β) provide the ligand specificity (*4*). The invariant dimers, including CD3 ϵ-γ, CD3 ϵ-δ, and ζ-ζ (*3, 5, 6*), are probably essential for signal transduction, as demonstrated by mutational analysis of the cytoplasmic tail of ζ (*7*). This domain of ζ can mediate the signaling events associated with TCR-mediated activation when expressed in a chimeric transmembrane protein (*8–10*). Two observations, however, suggest that ζ alone does not account for all of the func-

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