New Aspects of Avian Origins: Roundtable Report

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Introduction

The convening of the fourth International Meeting of the Society of Avian Paleontology and Evolution (SAPE) in the year 1996 is significant in that it coincides with the anniversary of several important dates in the history of the debate on the origin of birds. It marks the seventieth anniversary of the publication of Gerhard Heilmann's (1926) *The Origin of Birds,* a volume that established the orthodox view—that birds descended from basal archosaurs in the Triassic—for the next 50 years. Furthermore, 1996 marks the twentieth anniversary of the publication of John H. Ostrom's (1976) magnum opus "*Archaeopteryx* and the Origin of Birds," a comprehensive treatment arguing cogently that *Archaeopteryx* and all other birds are derived from coelurosaurian theropod dinosaurs. Finally, 1996 is the tenth anniversary of the publication of Jacques A. Gauthier's (1986) paper "Saurischian Monophyly and the Origin of Birds," a widely cited work that, among other things, offered critical cladistic support for the theropod affinities of birds.

This paper is not intended as a review of avian origins but rather as a report of the proceedings of an SAPE roundtable discussion organized by Peter Wellnhofer and moderated by myself on 7 June 1996. I was charged by Dr. Wellnhofer to provide the roundtable discussants with a brief overview of current notions on the origin of birds and then present several topics for discussion. I will first expand somewhat on the overview of current opinion to enable readers with less background to follow the discussion. Then the discussion topics will be introduced and their rationale presented. The relevant portion of the ensuing roundtable discussion will be reported after the introduction of each topic. The discussion itself was fairly wide-ranging, and participants often commented on more than one discussion topic. As a result, I will not present the report in its strict chronological order, but rather in the order of the discussion topics. Participants were aware that the proceedings were being recorded on audio- and videotape for subsequent report in this volume. Quotes herein are direct transcriptions from the audiotape, with trivial editing (e.g., deletion of false starts or midstream rephrasing) to enhance flow. Paraphrasings also derive from the audiotape.

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Overview of Current Opinion on the Origin of Birds

As mentioned, it is beyond the scope of this report to review the history of the debate. I previously provided a summary up through the late 1980s (Witmer, 1991), and Feduccia (1996) brought the review up to the present. The modern debate is typically characterized as a trio of hypotheses—the "pseudosuchian thecodont" hypothesis, the crocodylomorph hypothesis, and the theropod hypothesis—with theropod relationships holding sway and the other views decreasing somewhat in popularity. Several important developments have arisen in the intervening years, however, suggesting that opinion has not fully consolidated around the conventional theropod hypothesis. It is not the intent herein to provide a critical evaluation of these hypotheses but rather simply to present a thumbnail sketch and provide references.

1. Relationships with basal archosauriforms ("pseudosuchian thecodonts," to use the old paraphyletic taxonomy) were suggested originally by Broom (1913), and this was the idea popularized by Heilmann (1926). The basic premise is that Triassic archosauriforms, such as *Euparkeria,* are "sufficiently primitive" to have been ancestral to birds (and to other groups of archosaurs, as well). Although revived by Tarsitano and Hecht (1980; see also Tarsitano, 1991), the idea was widely criticized, particularly by supporters of theropod relationships (e.g., Thulborn and Hamley, 1982; Gauthier and Padian, 1985), for being uninformative and for offering few or no supporting synapomorphies. It had seemed that this view had passed away—principally because it was so nonspecific—until a recent paper by Welman (1995), who proposed numerous synapomorphies from the basicranial region of the skull, suggesting that *Euparkeria* is closer to avian ancestry than anyone ever thought.

2. A close relationship with crocodylomorphs, such as the Triassic form *Sphenosuchus,* was originally proposed by Walker (1972) and was supported by L.D. Martin (e.g., 1991) and

his students (see Witmer, 1991, for references). Supporting characters included aspects of tympanic pneumaticity, cranial circulation, and dental morphology and replacement. The crocodylomorph hypothesis was challenged on a number of counts (Gauthier, 1986) and received an apparent deathblow when Walker (1985) himself apparently recanted. Interestingly, Walker (1990, pers. comm., 1995) essentially recanted his recantation and offered renewed support for avian relationships with crocodylomorphs.

3. Nonarchosauriform archosauromorphs, such as the Triassic form *Megalancosaurus,* have been suggested to be close to avian ancestry by a number of authors (e.g., Hecht and Tarsitano, 1982; Martin, 1983; Tarsitano, 1985, 1991), most forcefully by Feduccia (1996; see also Feduccia and Wild, 1993). In all formulations, the origin of birds is tightly linked with the origin of flight, which is presumed to have required an initial arboreal phase. Therefore, it is reasoned, because avian ancestors must have been small and quadrupedal, bird-like forms, such as *Megalancosaurus* (and also *Longisquama, Cosesaurus,* or *Scleromochlus*), make good models for avian ancestors (Feduccia and Wild, 1993; Feduccia, 1996).

4. Theropod dinosaurs are certainly the group most commonly cited as being involved in the origin of birds (Witmer, 1991; Chiappe, 1995); however, the specific nature of the relationship, that is, which specific group of theropods is closest to birds, remains controversial. Ostrom (1976) proposed that dromaeosaurid coelurosaurs, such as *Deinonychus* and *Velociraptor,* were closest to birds based on a large suite of derived characters, principally from the manus and pelvic limb. This hypothesis received cladistic support from Padian (1982), Gauthier (1986), and Holtz (1994) and is the most commonly encountered version of the theropod hypothesis. Alternate versions differ in which clades are hypothesized to be the sister group of *Archaeopteryx* and/or other birds (see Witmer, 1991, for additional references): coelophysoid ceratosaurians such as *Syntarsus* (Raath, 1985), troodontid coelurosaurs (Currie, 1985, Paul, 1988), bullatosaurs (troodontids+ornithomimosaurs) (Thulborn, 1984), or oviraptorosaurs (Elzanowski, 1995, this volume). Sorting out this confusion will require a comprehensive and up-to-date phylogenetic analysis of Coelurosauria, itself involving a very careful analysis of many characters.

5. Under the broad heading of "the theropod hypothesis" is G.S. Paul's unique formulation (Paul, 1984, 1988). In Paul's view, not only are birds phylogenetically nested within Theropoda, but in fact some forms traditionally interpreted as nonavian theropods are actually secondarily flightless "protobirds." Paul (1988) envisioned a lineage of protobirds beginning in the Jurassic with *Archaeopteryx* and becoming even more bird-like in the Cretaceous, culminating in true birds (Metornithes, to use Chiappe's (1995) terminology). Along the way, the protobird lineage repeatedly gave off clades of terrestrial, secondarily flightless forms, such as Dromaeosauridae, Oviraptorosauria, Ornithomimosauria, and Troodontidae. For support, Paul (1988) cited characters from the skull and pelvic limb and offered additional evidence at the 1996 SAPE conference. This hypothesis has received scant attention in the literature.

6. A related notion is G. Olshevsky's (1994) "Birds Came First" (BCF) theory. This hypothesis suggests that the avian lineage is a truly ancient one. That is, archosaur phylogeny is characterized by a "central line" of persistently arboreal, quadrupedal "dino-birds" that, beginning in the Permian, continuously gave off branches of terrestrial archosaurs throughout the Mesozoic Era. These secondarily terrestrial clades went on to become the various clades of archosauriforms (e.g., proterosuchians, aetosaurs, sauropodomorph dinosaurs, etc.). Forms like *Megalancosaurus* and *Longisquama* are very close to this central line and never left the trees. This central line of arboreal dino-birds became progressively more bird-like through time and thus so did their terrestrial descendants. Theropods are on the central line, and thus, as in Paul's (1988) formulation, the Cretaceous bird-like theropods are deemed secondarily flightless forms. Also like Paul's hypothesis, Olshevsky's ideas have been virtually ignored in the literature.

The Roundtable Discussion

Six major topics were presented at the roundtable for discussion. The topics were chosen to stimulate debate, to examine critical issues, and, it was hoped, to reach agreement on at least some points. Again, each topic is briefly outlined below to set up the ensuing discussion.

1. The Central Role of *Archaeopteryx* in the Debate

The history of the debate on avian origins, almost since its inception, has been focused on *Archaeopteryx.* In fact, *Archaeopteryx* has been the key player in not just the origin of birds but in virtually all ancillary debates: the origin of flight (Rayner, 1988; Feduccia, 1993, 1996; Herzog, 1993), the origin of feathers (Parkes, 1966; Dyck, 1985), the origin of endothermy (Ruben, 1995), and others. An entire conference and the resulting volume (Hecht et al., 1985) were devoted to *Archaeopteryx* and its impact on these questions. Moreover, *Archaeopteryx* has importance beyond its technical significance as a symbol of organic evolution. As Ostrom stated during the roundtable, "the Berlin specimen [of *Archaeopteryx*] is the most valuable and most famous specimen of anything."

Given this historically central role, the discussion topic posed to the roundtable participants was whether or not this role is deserved. The first sentence of Ostrom's (1976:91) paper states, "The question of the origin of birds can be equated with the origin of *Archaeopteryx,*" which clearly articulates the feeling that if we can understand *Archaeopteryx,* we will automatically understand the origin of birds (and the origin of flight, etc.). The avian status of *Archaeopteryx* is an unstated assumption of most analyses. The worry is that if all argumentation is founded on this assumption and this assumption is

proved questionable or even invalid, then an enormous amount of scientific discourse will have to be called into question. The stakes are quite high. Interestingly, the history of the debate (Witmer, 1991) shows a persistent minority arguing that *Archaeopteryx* may not be part of the true avian clade but rather is a feathered dinosaur (e.g., Lowe, 1944; Thulborn, 1975, 1984; Thulborn and Hamley, 1982; Barsbold, 1983; Kurzanov, 1985). The intent of raising the issue about the central role of *Archaeopteryx* was to nurture healthy skepticism and to offer the opportunity to reinforce (or dispute) its avian status.

The discussion opened with G.S. Paul taking up the issue he presented in his poster and abstract, namely, that *Archaeopteryx* is skeletally a small dromaeosaurid and perhaps not a true bird at all. Paul began by doubting that *Archaeopteryx* had the features of avian craniofacial kinesis suggested by Elzanowski and Wellnhofer (1996), citing the presence of a complete postorbital bar and a strong maxillary-lacrimal contact, both of which would prevent intracranial mobility; furthermore, Paul questioned their interpretation of bird-like features in the pterygoid. "Years ago when I saw the Eichstätt skull," Paul continued, "I thought that I saw an essentially theropod skull, and I believe that with the newest skull this is, in most ways, truer than I ever thought. ... I don't really see very much evidence of anything avian in the skull of *Archaeopteryx.* Except, as Elzanowski and Wellnhofer [1996] have pointed out, apparently the palatine is fairly avian [in being] triradiate and having a small palatine hook [i.e., the vomeropterygoid or choanal process]. But even there, some theropods get very close to that. For example, dromaeosaurs have virtually no fourth process, the maxillary process of the palatine. Postcranially, again, *Archaeopteryx* is very, very similar to dromaeosaurid theropods. The main features that are avian are in the forelimb and, as pointed out today [in Zhou and Martin's talk], particularly in the wrist and hand—and those are features associated with flight. I hadn't really realized until very recently how extremely similar *Archaeopteryx* is to dromaeosaurs in very detailed characters." To illustrate this point, Paul distributed handouts derived from his poster and led the participants through the intricacies of a single character, the twisting of the paroccipital process, which is very similar in *Archaeopteryx* and dromaeosaurids like *Velociraptor* and is unlike other archosaurs, with perhaps the exception of *Mononykus.* "This is what we're getting down to now," Paul continued. "We're getting down to little tiny details shared by dromaeosaurs and *Archaeopteryx.*"

L.M. Witmer suggested that Paul's comments primarily provided "further evidence, I think many of us would say, supporting that birds are related to small theropods, in particular dromaeosaurs. [But the issue is] not necessarily what are the features that *Archaeopteryx* shares with dromaeosaurs, but what are the features that *Archaeopteryx* shares with other birds?" A. Elzanowski responded that *Archaeopteryx* has "very well-defined avian characters in the skull," such as those associated with the palatine and pterygoid. He went on to enumerate features in *Archaeopteryx* that are unique and that set it apart from dromaeosaurids. For example, the pterygoid of *Archaeopteryx* is "so different from a typical theropod or dromaeosaurid pterygoid that we [he and Wellnhofer] had problems, I admit, in identifying what is the left and what is the right element. No one would have any problems of this sort with [theropods given] John Ostrom's excellent documentation of dromaeosaurids. ... The [pterygoid] wing that Greg [Paul] wants to see as an ectopterygoid process is certainly not an ectopterygoid process. ... The quadrate part of the pterygoid is radically, dramatically different from the dromaeosaurids. ... The skull is in many characters dramatically different from any known theropod. ... The nasal cavity has very peculiar structures that are very difficult to compare with anything known so far. The pterygoid has an absolutely peculiar longitudinal division which is very hard to interpret and to compare with anything else." Elzanowski argued that molecular systematics provides insight into the importance of weighing characters, such that "characters like bending of the paroccipital process are simply not comparable, and can never outweigh a radical, dramatic difference in, for example, the palatine bone, which is definitely avian in *Archaeopteryx* and is clearly theropodan in dromaeosaurids." Furthermore, he suggested that the presence of an avian palatine reflects significant transformation of the skull and evolution of an avian kinetic apparatus.

J.H. Ostrom argued passionately for the significance of the specimens of *Archaeopteryx,* yet he also noted that "the magnitude of Earth's history is enormous. With a handful of specimens, you think you're going to draw conclusions about who evolved from whom?" In a similar vein, K.C. Parkes offered, "With *Archaeopteryx* we have a snapshot—a snapshot of a brief moment in time. ... A hell of a lot of things must have happened between the time of our still arguable ancestral form [and *Archaeopteryx*]. ... We have absolutely no evidence of what happened up to the point of that snapshot in time, which means we have to take *Archaeopteryx* for what we have. ... The argument back and forth—is it a bird or not—seems to me almost fruitless because we don't know what came [even] half a million years before *Archaeopteryx.* So that to some extent, all of the conjecture as to where *Archaeopteryx* came from is going to be very fruitless until we can find something that's a lot closer to *Archaeopteryx* in time than anything we have now."

The role of *Archaeopteryx* continued to be debated by the participants but as part of other discussion topics, which appear in their appropriate contexts.

2. The Role of the Cretaceous Avian Radiations in the Debate

Certainly part of the reason *Archaeopteryx* has been so important is that for very many years it had been almost the only relevant Mesozoic bird (*Hesperornis* was too aberrant and *Ichthyornis* was too "modern" to be pertinent). With the numerous new discoveries of Early Cretaceous (perhaps even Late Jurassic) birds in Spain and China, the database has changed dramat-

ically. Because most analyses (e.g., Chiappe, 1995; Sanz et al., 1995) suggest that these birds are more closely related to modern birds than is *Archaeopteryx,* what relevance do these new discoveries hold for the debate on avian origins?

The discussion began with L.M. Chiappe, who suggested that "the role of the Cretaceous avian radiations, in my point of view, is very clear. Without disregarding the data that *Archaeopteryx* provides, I think that we actually don't need *Archaeopteryx* right now, for example, to support the idea that birds are descended from theropod dinosaurs. ... We have enormous support from this Cretaceous radiation." Likewise, P.C. Sereno argued for the critical role played by the new discoveries of Cretaceous birds: "Recently, even aside from these possible Late Jurassic–earliest Cretaceous forms, new birds have presented other combinations of characters that include even more advanced avian characters while still retaining things like gastralia and things that we've never seen in bird-like creatures before."

Some participants saw the Cretaceous avian radiations as helping to refine and redefine the role that *Archaeopteryx* plays in the debate. For example, Elzanowski suggested that "barely anything points so much to the central role of *Archaeopteryx*—its central position in [the] evolution of birds—than this record of *Sinornis* and *Confuciusornis*. [*Sinornis* is] perfectly intermediate between *Archaeopteryx* and more modern birds. ... So, if let's say *Sinornis* is intermediate between modern birds and *Archaeopteryx,* therefore, by purely logical reasoning, *Archaeopteryx* has to be central to the evolution of birds in morphological terms." For Sereno, the combination of *Archaeopteryx* and the Early Cretaceous birds presents "really a nice phylogenetic situation. I think for a cladist to look at *Archaeopteryx,* it additionally presents a strong argument for the origin of birds because it has so few autapomorphies. When you put it up on a cladogram, you try to see what are the characters that are unique to itself and to help to map its phylogenetic information. There are so few that we almost want to call it a metataxon (something that you can't actually link the specimens together by [apomorphic] features). I think that's the important thing, to reiterate what Luis [Chiappe] is saying, that we've got confirmatory evidence from other animals." G.S. Paul responded that "it is very possible that morphologically *Archaeopteryx* basically is a theropod dinosaur with wings. ... It is very possible that *Archaeopteryx* maybe was allied with dromaeosaurs or was a completely independent development from birds. On the other hand, what Paul [Sereno] just said is also true—it's so primitive that it could be at the base of the bird radiation. ... In a way, we really don't know whether *Archaeopteryx* has a central role or not—we do not have the information yet."

3. The Theropod Hypothesis and the "Time Problem"

Although the theropod hypothesis has been the most popular one for more than twenty years, it has always faced what may be regarded as "the time problem" (Witmer, 1995; see also Feduccia, 1996), namely, the most bird-like of the nonavian theropods (e.g., dromaeosaurids, troodontids, oviraptorosaurs) are younger in age than *Archaeopteryx.* If the conventional hypothesis is correct, then birds and nonavian coelurosaurs diverged in at least the Jurassic. Where, for example, are the Jurassic dromaeosaurs? How disturbed should we be by this discordance in the fossil record? Does it severely damage the theropod hypothesis, as has been suggested (Tarsitano, 1991; Feduccia, 1994, 1996)?

The discussion of this topic was limited. Sereno, who has studied the temporal ranges of theropod clades in conjunction with the pattern of phylogenetic branching, acknowledged that "there is a time discordance between *Archaeopteryx* and its nearest sister group. But when you look at the overall phylogeny of theropods, there are many time discordances—but also many missing lineages with much greater length than that actually. For example, if we look at the origin of coelurosaurs, we now have radiometrically dated allosaur-like animals for the Lower Jurassic. We know that there was a coelurosaur lineage at the base of that radiation for which we have no evidence for the Jurassic, essentially until the Late Jurassic. So, we're missing maybe 20–30 million years of early coelurosaur evolution before we get to the point where we were talking about *Archaeopteryx* and these other things. So, it's not that unusual. It seems that small theropods in general are your worst case extreme for taphonomists, because you don't have the option usually of lake beds or near-shore marine sedimentary localities, but neither do you have the size that will often carry you through in a fluvial environment. So, you fall in-between the cracks in a very poor record."

4. The Significance of *Protoavis* for the Debate

From the time of its discovery, *Archaeopteryx* was regarded as both the oldest and the most primitive bird. Reports of Triassic avian remains from Texas (Chatterjee, 1987, 1991, 1995, this volume) would appear to challenge one or both of these claims. According to Chatterjee's (1991) cladogram (see also Kurochkin, 1995), *Protoavis* is closer to the modern radiation than is *Archaeopteryx.* In other words, *Archaeopteryx* would remain the basal member of Aves, but not the oldest. Thus, what is the significance—even relevance—of *Protoavis* for the debate on avian origins? Obviously it would make the time problem of topic three, above, much worse, telescoping much of theropod cladogenesis into the Norian or even Carnian. Otherwise, *Protoavis* might behave phylogenetically much like the components of the Cretaceous avian radiation (topic two, above).

The discussion began with S. Chatterjee, who saw the time problem as less of an issue, suggesting that "we're caught up in a stratophenetic approach. ... We are very content with *Archaeopteryx*—this is the primitive one. You can derive anything from it. When the new evidence comes, look at it. Look at the bones. I think what it tells us is that, like mammals, there was a

very bush-like radiation of birds." Chatterjee argued that the real significance of *Protoavis* resides in its prospects for establishing a skeletal definition of birds: "Once you define it, then there is no problem. For *Archaeopteryx* or for birds it is really a circular argument: we are defining on feathers. Do we define mammals on hair? No. ... We need some practical, tangible evidence preserved in the fossils so that we can call it 'bird.' Once you define it, then you can see whether *Archaeopteryx* falls under the definition or not. ... The time has come: we have to give the osteological definition of birds. For that matter, I think *Protoavis* really has a much, much better chance. You can define birds on the basis of the quadrate. You can define birds on the basis of the cheek region. ... If you can document that the orbit and the two temporal openings are confluent, it *is* a bird."

Sereno stated that the significance of *Protoavis* cannot be adequately assessed until the professional community takes a serious approach to the fossils: "It seems that most people ignore *Protoavis,* and I think that this is a sad situation. I think there's a lot of very different opinions about what *Protoavis* is, and some of these have been aired. [But] if we're going to move on the significance of *Protoavis,* it probably would be in having some type of a consortium with the fossil material, with people actually commenting on what they think it is in a serious-science forum."

5. The Origin of Birds Versus the Origin of Flight

In some formulations (Tarsitano, 1991; Feduccia, 1993, 1996; Feduccia and Wild, 1993), the origin of flight and the origin of birds are inextricably united: flight "from the ground up" with the theropod hypothesis and flight "from the trees down" with more basal archosaurs. The protocol appears to be to develop a concept of the hypothetical proavis based on one's notion of the origin of flight and then survey the animal kingdom for a match; that is, the functional inference precedes the phylogenetic inference. The intent of this topic is not to examine the origin of flight, but rather to discuss the necessity of coupling these two issues. In other words, what is the relationship of phylogenetic inference to functional inference?

The discussion began with Elzanowski, who proposed, "the strict coupling of theropod/'from-the-ground-up' and alternative-hypotheses/'from-the-trees-down' is not really warranted. I think that the discussion of the taxonomic origin of birds should be decoupled from the mechanics—the evolutionary mechanism—of the origin of flight. As all of us probably agree, we really don't know, in a strict sense, the ancestor of birds—we can't agree which are the closest theropod relatives of birds. We have no idea [of their] size or what those ancestors looked like. We know that they certainly were smaller than basically all the dinosaurs we have fossils of." Elzanowski argued that, as observed in mammals, small theropod dinosaurs would have had much more "flexible ankles" than large dinosaurs. This is "a known generalization. ... There is no reason to question that there were arboreal or slightly arboreal theropods that would just climb on the tree or run on the tree trunk and [then] just jump and glide from the tree trunk."

Chiappe agreed that the two should be decoupled, saying, "The kind of data that we have is completely different. For the origin of birds, [it] is exclusively phylogenetic. We have a lot of data. We have fossils we can measure, look at, and examine. The origin of flight is a totally different question—a very interesting one, but the kind of data that we have is certainly ten times more speculative. ... First, we should come up with an idea, a notion, about the origin of birds, ... and then try to see how we can explain the origin of flight within the framework of that particular idea." Sereno likewise argued "that the two are very separate, because when you start looking at the problem phylogenetically, only some of the characters that are linking these animals together into an evolutionary sequence actually are related to flight. Some of the most interesting things are the characters that were co-opted but were not evolved for flight in the first place. We have the extraordinary opportunity, with the great functional work that's being done and a series of fossils, to go at this functional transformation like we cannot in the case of bats and pterosaurs. We can actually tease apart the functional sequence, but all of the characters are not related to that functional sequence, so the two are pretty separate."

P. Wellnhofer provided some important cautionary remarks about, again, over-reliance on *Archaeopteryx,* commenting that "we have to be careful in our conclusions. I think it's not so important what lifestyle *Archaeopteryx* as an animal really had. Maybe [it] could even climb or sit on a tree or on a tree branch or something like that. I think what's more important is the general architecture of the skeleton. The lifestyle of *Archaeopteryx* [itself] can be quite different from what we suggest."

6. The Validity of "Nonstandard" Hypotheses

As in probably all areas of human endeavor, science tends to eschew the iconoclastic in favor of familiar things from familiar sources. In the present case, the "nonstandard" views of Paul and Olshevsky seem to be examples of this phenomenon in that they reverse the typical ancestor-descendant relationship, derive from individuals that are outside the "fold" of university and museum professionals, and have not been published in the conventional outlets. As mentioned, these views have been almost totally ignored. Ironically, both views agree with the current orthodoxy that birds and theropods are very closely related and, moreover, present the advantage that the time problem disappears. The intent of this topic is to examine the status of these views in the current debate.

The discussion was limited to a statement by L.D. Martin: "One of the things about this conference that I've found extremely interesting is how many of the papers that were presented today could be taken to support Gregory Paul's so-called 'nonstandard' hypothesis. I would say he's getting so much support that we can view it as a school—'the Paulian

School of Bird Origins.' The only thing I see that it lacks for a confirmation would be the discovery of a Cretaceous dinosaur with enlarged feathers... and I would really think that we would have very strong support for Paul's viewpoint."

Recapitulation and Conclusions

Perhaps the best quote from the roundtable came from S.L. Olson: "There is no hypothesis involving the origin and evolution of birds that's too ridiculous that somebody won't propose it." This sentiment was shared by many of the participants, although—and this is the interesting part—there would not be much agreement as to which hypotheses were the ridiculous ones. The goal of the roundtable was not to establish winners and losers, or to be able to come away with a broad consensus on avian ancestry. The goal was to raise issues, discuss them openly, and establish some common ground, and in this the roundtable was very successful.

The role of *Archaeopteryx* received a rare critical appraisal. There was general agreement that *Archaeopteryx* will continue to merit a crucial role in not only this debate but in all the debates associated with the early radiation of birds. In an important departure from the past, however, *Archaeopteryx* may slowly be heading toward a more appropriate position as only one of a number of important fossil taxa. The rapidly growing number of Early Cretaceous (and perhaps even Late Jurassic) discoveries, some species of which are represented by dozens of complete skeletons with feathers, are tremendously helpful in reducing the weight of inferences that *Archaeopteryx* must bear. Furthermore, these Cretaceous fossils provide important corroborating information with regard to the origin of birds such that *Archaeopteryx* apparently could be dropped from many analyses with little resultant change in the phylogenetic pattern of avian ancestry. Several synapomorphies of *Archaeopteryx* and "true" birds were discussed. Nevertheless, the status of *Archaeopteryx* as a true bird was challenged by other participants, and, given the controversial status of a number of taxa discussed at the conference (e.g., "protobirds," *Mononykus,* oviraptorosaurs, new Malagasy fossils), perhaps it is indeed prudent to exercise caution about all taxa positioned phylogenetically near that transitional nexus. For many participants, it is likely that the roundtable ultimately did little to diminish either the avian status or the importance of *Archaeopteryx.* For others, the phylogenetic position of at least *Archaeopteryx* remains somewhat more uncertain. As for myself, I continue to regard *Archaeopteryx* as the basal member of Aves, while at the same time recognizing that I have been wrong before.

As mentioned above, the recent discoveries of indisputable Cretaceous birds were widely seen as contributing very important new data for the origin of birds. They confirm findings previously based solely on *Archaeopteryx* and provide new insights as well. The time problem facing the theropod hypothesis was discussed, and it was pointed out that the fossil record is rife with similar (and even worse) time discordances and that a stratophenetic approach is inappropriate. Perhaps the broadest level of agreement was that the functional issue of the origin of flight needs to be clearly separated from the phylogenetic issue of the origin of birds, although the discussion perhaps was hampered by the absence of several of the chief proponents of the linkage of these issues. Nevertheless, several participants voiced strong opinions that the issue of phylogenetic origin logically and methodologically precedes the exploration of models on the origin of flight. There was little focused discussion on what we should do with nonstandard hypotheses such as those of Paul and Olshevsky, although it was clear that Paul's ideas received an open hearing with perceptions ranging from receptive to skeptical.

In general, there was virtually no discussion of any hypotheses other than the theropod hypothesis, which received strong support from several participants. This situation probably genuinely reflects the broad acceptance that this notion has, but it probably also reflects the fact that several key proponents of alternative views were not in attendance, whereas most of the theropod principals were present. There was only passing discussion of the alternate versions of the theropod hypothesis with the only notable outcome being the survival (even thriving) of Paul's protobird hypothesis.

Finally, it is worth reporting that the roundtable was remarkably noncontentious. Participants listened patiently to the views of others, offered their responses with often amiable good humor, and generally seemed receptive to different ideas. That is not to say that strong views were not expressed, but only suggests that the tenor of the debate has moderated and moved onto a more professional and thoughtful level.

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Storrs L. Olson
EDITOR

Peter Wellnhofer, Cécile Mourer-Chauviré, David W. Steadman, and Larry D. Martin
ASSOCIATE EDITORS

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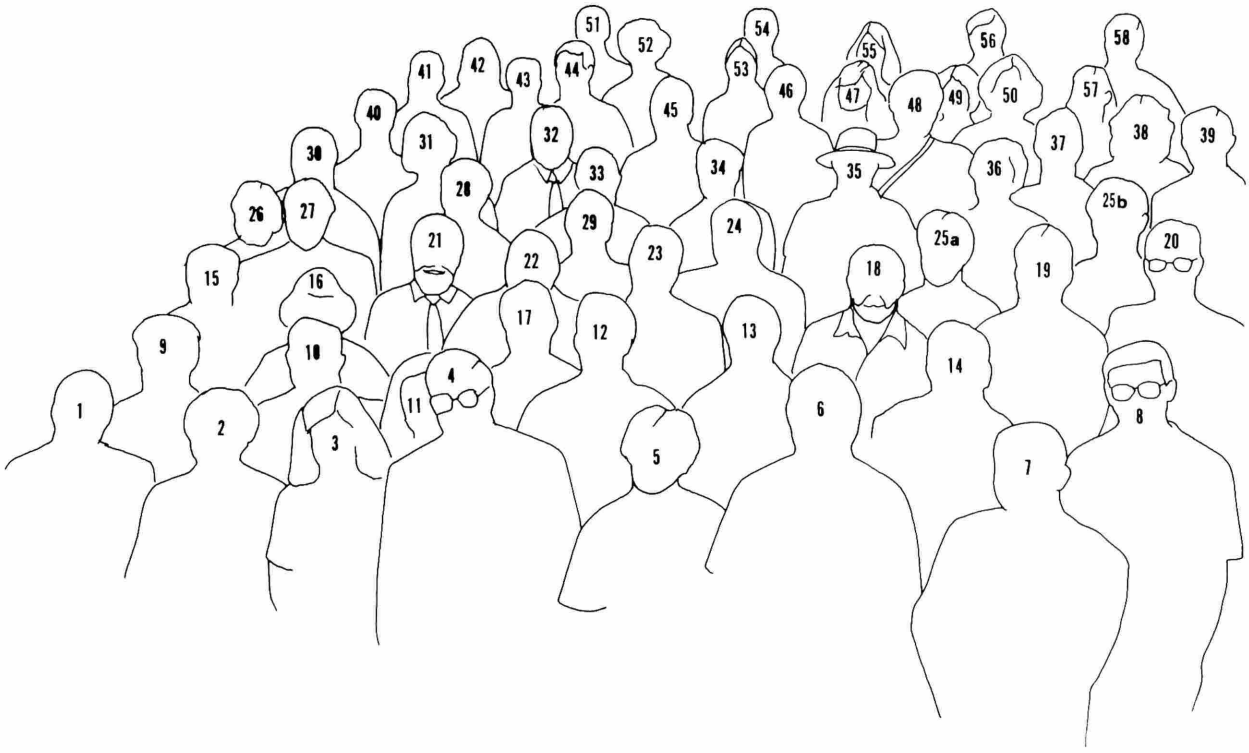
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FRONTISPIECE.—Participants in the Fourth International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 5 June 1996.

1. Peter Wellnhofer (Munich, Germany)
2. Ingrid Wellnhofer (Munich, Germany)
3. Helen James (Washington, D.C.)
4. Storrs Olson (Washington, D.C.)
5. Cécile Mourer-Chauviré (Lyon, France)
6. Kenneth Campbell (Los Angeles, California)
7. Stefan Peters (Frankfurt, Germany)
8. Zhonghe Zhou (Beijing, China)
9. Lianhai Hou (Beijing, China)
10. John Ostrom (New Haven, Connecticut)
11. Virginia Naples (DeKalb, Illinois)
12. Lawrence Witmer (Athens, Ohio)
13. Peter Houde (Las Cruces, New Mexico)
14. Paul Bühler (Gschwend, Germany; deceased, 16 July 1996)
15. Joseph M^{c}Kee (Palmerston North, New Zealand)
16. Sylvia Hope (San Francisco, California)
17. Jean Martin (Lawrence, Kansas)
18. Gregory Paul (Baltimore, Maryland)
19. Bartomeu Seguí (Ciutat de Mallorca, Spain)
20. David Parris (Trenton, New Jersey)
21. Evgeny Kurochkin (Moscow, Russia)
22. Larry Martin (Lawrence, Kansas)
23. Herculano Alvarenga (São Paulo, Brazil)
24. Kenneth Parkes (Pittsburg, Pennsylvania)

25a. Ewan Fordyce (Dunedin, New Zealand)

25b. Hiroshige Matsuoka (Kyoto, Japan)

26. Charlie Magovern (Boulder, Colorado)
27. Luis Chiappe (Los Angeles, California)
28. Kraig Derstler (New Orleans, Louisiana)
29. Craig Jones (Dunedin, New Zealand)
30. Ralph Chapman (Washington, D.C.)
31. Diego Rassman-Gutman (Washington, D.C.)
32. Felix Dzerzhinsky (Moscow, Russia)
33. Per Ericson (Stockholm, Sweden)
34. Richard Zusi (Washington, D.C.)
35. Phil Millener (Chattanooga, Tennessee)
36. Mary Root (Albuquerque, New Mexico)
37. Marco Pavia (Turin, Italy)
38. Jorge Noriega (Diamante, Argentina)
39. Antoni Alcover (Ciutat de Mallorca, Spain)
40. Trevor Worthy (Nelson, New Zealand)
41. Walter Boles (Sydney, Australia)
42. Tom Stidham (Berkeley, California)
43. William Hilgartner (Baltimore, Maryland)
44. Richard Benson (St. Paul, Minnesota)
45. Andrzej Elzanowski (Wroclaw, Poland)
46. Darrel Tanke (Drumheller, Canada)
47. Pamela Rasmussen (Washington, D.C.)
48. Tommy Tyrberg (Kimstad, Sweden)
49. Pippa Haarhoff (Capetown, South Africa)
50. Gerald Mayr (Berlin, Germany)
51. Steven Emslie (Wilmington, North Carolina)
52. John Stewart (Cambridge, United Kingdom)
53. Jenna Boyle (Gunnison, Colorado)
54. David Steadman (Gainesville, Florida)
55. Joanne Cooper (London, United Kingdom)
56. John Becker (Edmonton, Canada)
57. Claudia Tambussi (La Plata, Argentina)
58. Alexandr Karhu (Moscow, Russia)

Registrants not shown:

Michael Braun (Washington, D.C.)
Rachel Burke (New Brunswick, New Jersey)
Sankar Chatterjee (Lubbock, Texas)
Adele Conover (Huntington, Maryland)
Alan Cooper (Washington, D.C.)
Catherine Forster (Stony Brook, New York)
Steve Gatsey (Providence, Rhode Island)
G.E. Goslow, Jr. (Providence, Rhode Island)
Michael Gottfried (Solomons, Maryland)
Kevin Middleton (Providence, Rhode Island)
Eleni Paxinos (Washington, D.C.)
Samuel O. Poore (Providence, Rhode Island)
Paul Sereno (Chicago, Illinois)
Wesley Sutton (New York, New York)
Patricia Wainwright (New Brunswick, New Jersey)
Luvia Zusi (Washington, D.C.).