

2. Project Description

2.1 Project Motivation and Main Goals

We aim to understand the flight mechanics and dynamics of pterosaurs, and related aspects of functional morphology, biomechanics and flight evolution. Pterosaurs evolved from small, stable flyers in the Triassic and Jurassic to become very large and very agile flyers in the Late Cretaceous. These highly derived pterodactyloids exploited their flexible membrane wing structure for flight control and propulsion.

The proposed work is motivated by the Stanford-National Geographic Pterosaur Replica Project (SNGP) described in subsection 2.3. SNGP was a one-year preliminary project focused on building an airworthy replica of *Anhanguera piscator* with current knowledge on pterosaur flight. This preliminary work has clearly shown the many open questions in this area, and the need for extensive and detailed research involving paleobiology, biomechanics, aeronautics, and aerodynamics.

The main questions we will address in this study are:

- How did large derived pterosaurs exploit aeroelasticity for control and propulsion?
- What are the probable bone, muscle and membrane properties related to flight?
- What muscle actuations and energy expenditures were needed to sustain flight?

To answer our questions successfully, a strong interdisciplinary project team is essential. Our team consists of experts in paleontology (with emphasis on evolutionary paleontology and functional morphology), biomechanics, aerodynamics and aeronautics, bird flight, computational mathematics, and mechanical design.

We focus particularly on *Anhanguera piscator*, a 5-meter wingspan pterodactyl for which extensive and high quality fossil material is available. In our study on the evolution of pterosaur flight mechanics we will include both basal and derived pterosaurs. Some paleontological evidence is available for wing planform and airfoil construction in some pterosaurs, but the evidence is conflicting. The primary questions to ask of the paleobiological evidence, therefore, relate to the empirical basis for reconstructing pterosaur wings, the limitations of knowledge, and a sensitivity analysis of possible configurations to determine consequences for aerodynamic performance.

We will address our research questions using a combination of theoretical work and physical experiments. Results from our planned studies of functional morphology and flight mechanics will feed into a complete biomechanical computer model of *Anhanguera piscator*. We will use this model to investigate necessary muscle actuation and energy expenditures, and derive probable representations of major muscle groups, bone and membrane properties. In return, the biomechanics study will be used to improve and correct functional morphology and flight studies. The results will be integrated into a flight simulator, and linked to an optimizer to determine best flight patterns depending on weather conditions and energy requirements. The proposal includes the design and building of a mechanical airworthy replica that we will throughout the study for testing control mechanisms and structural responses. These physical experiments are essential complements to the theoretical and computational studies.

The findings in this study will help to address a plethora of other questions related to pterosaur flight, including the implications of different models of wing-body and wing-hind limb attachment, and the role of the actinofibrils (fiber structures present in the membrane) in controlling wing performance. Specific project objectives are given in section 2.4.

2.2 Expected Innovations and Scientific Breakthroughs

2.2.1 Functional Morphology

A major strength in this work is the integration of functional morphology, evolutionary paleontology, flight mechanics, and biomechanics.

Late Cretaceous pterodactyloid pterosaurs were primarily large animals (wingspan 2-11 meters) that flew in very different ways from more basal pterosaurs. The “rhamphorhynchoid” pterosaurs of the Jurassic had long tails, which conferred dynamic stability while permitting a substantial degree of maneuverability (Wellnhofer, 1991; Witmer et al., 2003). The derived pterodactyloids, which were originally relatively small (wingspan <1 meter) lost the tail and reconfigured the wing, which permitted even better maneuverability. The more basal “rhamphorhynchoids” died out not long thereafter, and the Cretaceous history of pterodactyloids is principally a series of trends toward larger size, more soaring mechanics, and the iterated evolution of large and often bizarre cranial crests. A principal focus of this study is the functional morphology of the skeletal elements most involved in the generation of thrust and lift and the control of the wing.

The Cretaceous pterodactyloid *Anhanguera piscator* will serve as the “model animal” for this study. The 5m wingspan *Anhanguera piscator* is shown in Figs. 1 and 2. Extensive and high-quality fossils of this animal are available (Kellner and Tomida, 2000). High-resolution casts of the available specimens will be used to assess the origin and insertion of the major muscles that control the wing. Supplementary evidence comes from other pterosaur species for which these features are well understood (e.g., *Dimorphodon*: Padian 1983a, b; Bennett 1994, 1995). Although some major skeletal features changed during pterosaur evolution (see above), skeletal landmarks that document these transitions are preserved. This is also true for details of the fine structure of the wing, which are relatively uniform across pterosaurs (Padian and Rayner, 1993, Bennett 2000).

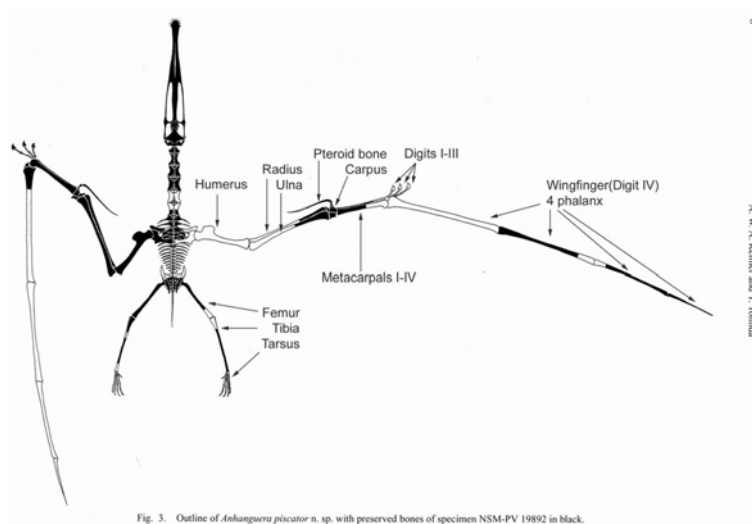


Figure 1. *Anhanguera piscator* skeleton (Kellner and Tomida, 2000)



Figure 2. Top, side views, *Anhanguera piscator* (courtesy John Conway)

From the origin and insertion areas of muscles, muscle force can be approximated, although there are some uncertainties about muscle histology and architecture. Following work by Hutchinson et al.

(2001), we will use sensitivity analysis to determine limits of variability of different models of muscle configuration. In practice, this will not be a substantial problem; the animal was obviously airworthy, and its size indicates that it was primarily a soaring animal that used flapping intermittently to provide thrust. Our focus will be first on the control of the wing in soaring: control of camber and pitch, aeroelasticity of the compound structure of bone, skin, and connective tissue that comprised the wing membrane, and functions of the various bones of the wing spar. We will then extend our scope to include flapping flight. In flapping flight different muscles come into play, and loads on muscles and skeletal elements of the spar are also unlike those in soaring.

One principal question in pterosaur biology is the shape, extent, and attachment of the wing membranes (Padian and Rayner 1993, Unwin 1999, Bennett 2000). Did they extend as far posterior as the hip, the thigh, or the ankle? Regardless of posterior extent, was the trailing edge straight or curved? Although a trailing edge tendon was apparently not necessary for flight control (Padian and Rayner 1993), evidence of it has now been adduced (Tischlinger and Frey, 2002). How would this tendon have interacted with the internal network of actinofibrils, the slender structural fibers arranged in a radiating pattern on the outer wing membrane, to manipulate the wing (Padian and Rayner 1993; Wellnhofer 1991)? Another question relates to mechanical properties of the actinofibrils, which are currently unknown, and their function in controlling membrane shape during flight.

Again, where paleontological evidence is limited, conflicting, or subject to differing interpretations (including the legitimate possibility of variation among taxa), our project will not have to make an a priori, ad hoc choice. We will use several wing models, representing reasonable reconstructions based on fossil evidence, to determine the various effects on aerodynamic performance. This kind of sensitivity analysis, of course, will not determine what the actual paleobiological situation was; rather, it will show what parameters, insofar as we are able to reconstruct them, would have had various kinds of consequences on the animal's flight.

As part of this project, we will integrate the analytic results of the various disciplines into a real-time flight and biomechanics simulation. An integrated visualization effort can help gain an intuitive understanding of the complex interactions among pterosaur bone, muscle, membrane, and ligaments, and the surrounding atmosphere while in flight.

2.2.2 Pterosaur Flight Mechanics

Pterosaurs, the first vertebrates to evolve powered flight, were long thought to be primitive flyers inferior to birds and bats. This perspective changed as a result of more recent studies of pterosaur morphology and flight mechanics (Bramwell and Whitfield 1974; Padian 1983a, b, 1987, 1991; Pennycuik 1988, Hazlehurst and Rayner 1992; Padian and Rayner 1993), including the recent Stanford-National Geographic Pterosaur Replica Project. Pterosaurs evolved from small, stable flyers to much larger and more agile flying creatures. The more derived pterosaurs were more dynamically unstable in flight, and probably used subtle and sophisticated flight control mechanisms involving span, sweep, dihedral and twist variations. Modern adaptive wing designs involve similar mechanisms (McMasters and Cummings 2004; Stanewsky 2000, 2001; Inman et al. 2001; Livne and Weisshaar 2003). Perhaps pterosaurs have the most to teach us regarding possible future aircraft development, not just in adaptive wing designs, but also in the design of effective membrane wings, advances in flight control mechanisms, and designs of effective flapping flight mechanisms, particularly in flying animals of great size (the largest known pterosaur is 50% larger in wingspan than the largest known fossil bird).

Anhanguera piscator and many other larger pterosaurs were predominantly soarers that used flapping intermittently for propulsion. The flexible-membrane wings of pterosaurs enabled them to exploit

aeroelasticity to control flight and achieve efficient propulsion. Efficient propulsion through wing flapping requires a carefully tailored distribution of lift, which in turn requires large changes in twist. Although such twist distribution may be achieved by direct actuation of the wing structure, many if not all changes in ideal twist may be achieved passively through aeroelasticity. This simplifies the control and, along with clear advantages associated with wing folding, may be an important evolutionary advantage for membrane wings. In addition, camber variations that arise naturally in membrane wings increase the section lift coefficients that are achievable without leading edge suction loss - an important consideration for efficient flapping flight (deLaurier, 1999; Birch et al. 2003, 2004; Dickinson et al. 1999; Dudley 2000; Kamakoti et al. 2000; Sane and Dickinson 2001, 2002; Dial et al. 1998). Subtle changes in membrane tension can produce significant changes in the distribution of lift over a pterosaur wing. The adaptive load redistribution was likely used for load alleviation, reducing bending moments in the pterosaur structure during maneuvers and gusts. It might also have been used to reduce vortex drag over a range of flight speeds, adapting wing twist passively to improve flight performance.

Constructive application of aeroelasticity may have also been a key aspect of pterosaur control. The reduction in roll damping due to passive aeroelastic interactions is essential for lateral maneuverability of these high aspect ratio wings. The variable twist also reduces adverse yawing moments at low speeds, enabling pterosaurs to fly without large vertical surfaces for yaw control.

The strongly nonlinear structural characteristics of pterosaur and other membrane wings pose challenges to existing analysis and design methods. In this project we will attempt to gain a deeper understanding of the nonlinear interactions between flow and flexible membrane structures by designing improved computational models to study and simulate these interactions. The calculation of pterosaur membrane wing aeroelasticity is more difficult than for conventional aircraft structures and many of the well-known methods for aeroelastic analysis are not applicable. This is caused by several features of pterosaur wing structure and aerodynamics. First, large camber and twist changes make typical linearized analysis of aerodynamics and structures inappropriate. Camber changes in particular can have a significant effect on the creatures' pitch control and are almost always ignored in conventional aeroelastic analysis. Second, geometric nonlinearities in the membrane wing structure also require a more general approach to computational aeroelasticity. This feature of membrane wings and sails - that they are floppy when unloaded, and much stiffer under load - is critical to estimates of performance and dynamics, but makes computations more difficult. And third, with low Reynolds numbers and sections close to separation, nonlinear aerodynamic models must be used to estimate loads and deflections (Kunz and Kroo, 2000)

The methodologies and codes developed in this project are not only important in the design of membrane wings, parachutes and sails, but also in the design of other structures that use flexible materials. One such example is the design of large building structures that rely on the use of very light membrane materials. The proposed detailed study of aeroelasticity has a strong potential application to small autonomous aircraft of interest for both military and civilian roles (surveillance, early detection of, e.g., forest fires, agricultural uses). Small Unmanned Aerial Vehicles (UAVs) with flexible surfaces and some flapping concepts have been pursued at NASA and DARPA over the past few years, but a full understanding of flexible active wings is not complete, especially at low speed flight (Kudva et al. 2002).

2.2.3 Biomechanical Model

The results from the studies in functional morphology and flight mechanics and dynamics will feed into a complete biomechanical model of the pterosaur as related to flight. The model will be developed in graphics-based software environment (SIMM, Fig. 3), developed at Stanford. We will use this model to investigate necessary muscle actuation and energy expenditures, and derive probable representations of major muscle groups, bone and membrane properties. In return, this study will be used to improve and correct, where necessary, functional morphology and flight mechanics and dynamics.

SIMM allows users to build models that accurately represent muscle force generation, bone geometry, joint kinematics, and movement dynamics. It lets users create, alter, and evaluate models of almost any musculoskeletal structure (Delp and Loan, 1995). A SIMM model consists of a set of rigid segments connected by joints. Muscles and ligaments span the joints, develop force, and accelerate movement. SIMM is used in over a hundred biomechanics laboratories around the world to provide a consistent framework for the development and testing of models to study human and animal movement.

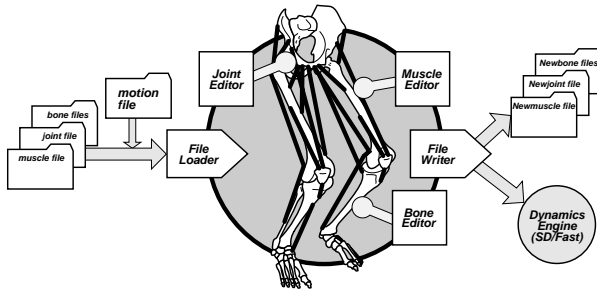


Figure 3. Structure of our musculoskeletal modeling software. SIMM allows users to build models that accurately represent muscle force generation, bone geometry, joint kinematics, and movement dynamics. SIMM's File Loader reads input files describing the bone surfaces, joint kinematics, and muscle-tendon parameters. Users can interactively edit a model using the Joint Editor, Muscle Editor, Bone Editor, and other tools. SIMM's File Writer creates an input file for SD/Fast, a dynamics engine for forward simulations.

As an example of its usefulness in paleontology, Hutchinson et al (2005) developed a 3D graphics-based model of the musculoskeletal system of *Tyrannosaurus rex* to estimate its abilities to walk (and whether it could run), and its performance at a range of speeds (Hutchinson 2004a, b). The model includes 10 degrees of joint freedom (hip to toe) and 33 main muscle groups crossing the hip, knee, ankle, and toe joints of the right hind limb (Fig. 4). This model was used to examine how the limb orientation (set of joint angles) of *T. rex* might have influenced the flexor and extensor moment arms (leverage) of its muscles. Sensitivity analyses of uncertain parameters, such as muscle origin and insertion centroids, explored how much the conclusions depend on the muscle reconstruction adopted, showing for which muscles the mechanics are most problematic to reconstruct. This information is important for determining how *T. rex* stood and walked, and how the muscles of a ~6000 kg biped might have worked in comparison with extant bipeds such as birds and humans.

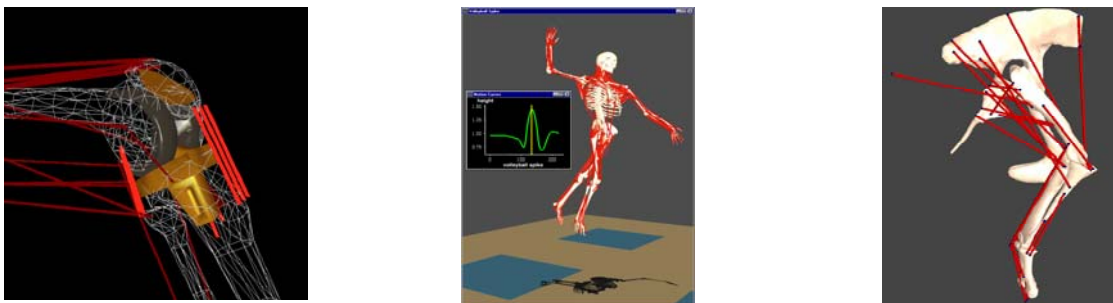


Figure 4. Biomechanical models developed in SIMM. A model of the human knee (left panel) has been developed and used to evaluate computational prototypes of knee implants (Piazza and Delp, 2001). A simulation of jumping (center panel) has been created to study the factors that affect jumping performance. A model of the hind limb of the *Tyrannosaurus rex* used to evaluate its locomotor capability (Hutchinson et al, 2005)

We will extend SIMM to generate computer models of the pterosaur flight musculature to examine their

capacity to actuate flight.

2.2.4 Integrated Flight Simulation

Results from our studies in functional morphology, flight mechanics and dynamics and biomechanics will be integrated into a flight simulator. The integrated visualization will help gain an intuitive understanding of the complex interactions between the flexible membrane wing, bones and muscles, and the surrounding atmosphere while in flight. The graphical flight simulation tool is an excellent means to excite scientific and engineering communities, as well as the public at large (outreach).

Dr. Eric Hallberg will provide the aeronautical engineering support (sub award) in the form of modeling, simulation, and visualization efforts for this part of the project.

The flight simulator will incorporate the algorithms and codes developed in this project for

- Analysis of nonlinear flow structure interaction, for gliding/soaring as well as flapping flight.
- Computation and visualization of forces on the structural elements of the pterosaur
- Flow computation and visualization. In addition to the codes developed in this research, existing Computational Fluid Dynamics software will be integrated to provide flow visualization.
- Computation and visualization of pterosaur motion during gliding and flapping flight
- Computation and visualization of muscle actuation and forces (SIMM)

The flight simulator will be built using multiple CPUs, with one or more CPUs running flight dynamics calculations, and others the visualization software. The computationally intense flight dynamics codes can then pre-compute data structures through the use of look-up-tables that are fed into the visualization tools, allowing real-time flight simulation.

The tool will include the essential ingredients to investigate flight of other pterosaur species, or related vertebrates (birds, bats).

2.2.5 Other benefits to the scientific and general community

Pterosaur flight is an intriguing topic that stimulates imagination and creativity, and appeals to the scientific and engineering community as well as the general public. This project offers excellent opportunities for scientific outreach. The current Stanford-National Geographic Pterosaur Replica project forms the spine of a 90-minute National Geographic documentary on pterosaurs and pterosaur flight, now in development, and featuring many of the principals involved in this project. This film will be released to international television in early 2006. The film and the national and international media attention that it will no doubt receive will provide an outstanding platform for public dissemination of this proposed work and related research. In section 2.6 we describe plans to attract and actively involve high school students and undergraduates through summer projects and academic courses, and the general public through an extensive museum exhibit and comprehensive website.

Besides being a very valuable tool for researchers, the biomechanics and flight simulation tools we propose to develop capture the imagination of a broad audience, some of whom may not have a deep background in paleontology or biology, such as K-12 students. They allow children and students to “see, experiment, and understand” long before the appropriate tools have been sufficiently developed for a deeper understanding of the individual disciplines.

2.3 Stanford-National Geographic Pterosaur Replica Project

2.3.1 Past Collaborative Projects

Collaborations between paleobiologists and aerodynamicists have a long history. As far back as 1914, J.W. Hankin and paleontologist D.M.S. Watson collaborated to understand better the flight of *Pteranodon* (Hankin and Watson 1914). Their study was a direct intellectual ancestor of the well-known Bramwell and Whitfield study on the biomechanics of *Pteranodon* (Bramwell, 1971a, b; Bramwell and Whitfield 1973, 1974). In 1984 the Smithsonian's Air and Space Museum commissioned Paul MacCready and his firm Aerovironment, Inc. to build a half scale flying replica of *Quetzalcoatlus Northropi* (Brooks et al, 1985, MacCready, 1984, 1985). Both Professors Ilan Kroo and Kevin Padian, Co-Pis on this proposal, were involved in this project. Flying without an aerodynamic tail structure, the replica relied on the use of forward sweep with wash-in at the wing finger joint to achieve pitch stability. Additional yaw control was added by using the head as a steerable forward fin, and by using the three small finger digits as drag devices (Jex 2000). While the MacCready robot was a significant technical achievement, it did not attempt to address the wing-membrane-hind limb question, and was also not intended to realistically model pterosaur flight mechanics and dynamics. New, high quality fossil finds (notably from the Cretaceous Santana formation of Brazil) and important recent work by Padian, Rayner, Bennett, Wellnhofer, Templin and other workers (Padian and Rayner 1993; Bennett 2001; Templin 2000; Wellnhofer 1991; Chatterjee and Templin 2004) have shed new light on the functional morphology and aerodynamic potential of this and related pterosaurs. Also, it is now apparent that aeroelasticity of the wing is a key feature of pterosaur flight that was exploited to provide efficient flight control and propulsion.

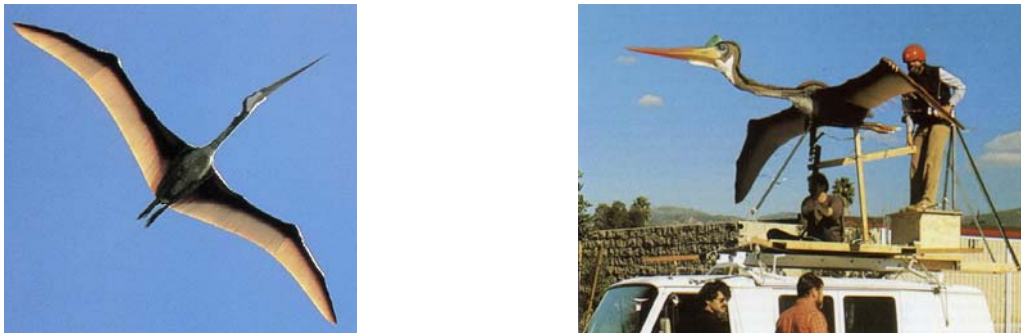


Figure 5. Paul MacCready's half-scale replica of *Quetzalcoatlus Northropi* (MacCready, 1984, 1985)

The Stanford – National Geographic Pterosaur Replica Project (SNGP) is the first project after Paul MacCready's to design and build a mechanical flying pterosaur replica. For reasons related to showing viewers the dynamics of paleontological exploration and discovery, it focuses in part on a partial skeleton of a pterosaur found in Niger during a National Geographic-sponsored expedition with paleontologist Paul Sereno. Because the fossil remains of this African pterosaur are incomplete and the specimen is a close relative of *Anhanguera piscator*, described in section 2.2.1, SNGP models its pterosaur replica on *Anhanguera piscator*.

The project involves the PI and co-Pis of this proposal, with the exception of Scott Delp, as well as several outstanding advisors in paleontology and aeronautics, including pterosaur experts Professor Christopher Bennett and Mr. James Cunningham, aeronautical engineers Paul MacCready and John McMasters from Boeing Co, and flapping flight expert Professor Jim deLaurier. Although not all listed as formal unfunded collaborators in this project, many of the experts advising SNGP will be supporting the current proposal.

2.3.2 Design of the mechanical replica of *Anhanguera piscator*

Building a flyable and controllable replica of the agile *Anhanguera piscator* is challenging. The uropatagium, if present, might have been used as a low effectiveness-high bandwidth pitch control and sweep as a highly effective low-bandwidth pitch control. In the replica, the tail is designed as a high speed pitch stabilizer and wing sweep as a pilot induced pitch control.

The head is destabilizing in yaw primarily. One of the control priorities has been to find a way to counteract this destabilizing moment in sideslip. Using LinAir, static linear lifting line software developed by Desktopaero Co., a few control strategies have been studied to create pure yaw. Asymmetric drag distribution, span changes, and weight shifts are among those studied. Changing the lift distribution anti symmetrically without inducing a rolling moment – known as the crow effect – seems to be a good candidate. However, because of the complexity of the aero-elastic interactions only flight tests can determine at this point the feasibility of these strategies.

The design work is carried out in three stages of increasing complexity. In stage 1, a 3m wingspan gliding model with rigid wings was built to test various control mechanisms that use wing tip movements. In stage 2, a 3m wingspan glider with a flexible and fully controllable membrane wing is tested. The camber and twist distribution of the wing is calculated with an integrated aerodynamics and structures code in order to give the desired shape under flight conditions. The coupled aerodynamics and structural studies helped find an appropriate low-energy position of the wing structure for gliding flight. It has also been found that the wing finger bones alone are not able to withstand 1-g level flight loads.

The wing membrane is designed to emulate the presence of actinofibrils (Figs. 6-8) and will be manufactured using modern sail-making techniques. In the course of the project, it became clear that the actinofibrils significantly alter directional stiffness of the membrane and act in compression. It is hypothesized that they had an important function in camber control. Flight tests are aimed to provide improved knowledge interactions among the wing finger, wing membrane, and other joints. In parallel, the design of the flapping mechanisms and the active head and tail controls are in development and will be integrated with the glide controls in the full-scale 5m replica.



Figure 6. Zittel wing membrane showing actinofibrils (from Wellnhofer 1991)



Figure 7. Detail Fig. 6



Figure 8. Replica wing made out of nylon monofilament emulating actinofibrils vacuum-bagged on polyester rip-stop cloth

A complete muscle sculpture of the creature (Fig. 9) was created at Hall Train Studios, Toronto, using references on crocodylian and avian anatomy. This sculpture aimed at giving a preliminary estimate of the volume and weight of the creature, and representation of the main muscle groups. For illustration purposes, Fig. 10 shows a biomechanical model of a human arm produced by SIMM.



Figure 9. Muscle cast of *Anhanguera piscator* as constructed by J. Conway, J. Cunningham and C. Bennett at Hall Train Studios, Toronto



Figure 10. SIMM biomechanical model picture of a human arm, courtesy of K. Holzbour and S. Delp. Muscles are represented by red cables clearly showing attachment points.

The preliminary work in SNGP has clearly shown us the need for extensive and detailed research involving paleobiology, biomechanics, aeronautics, and aerodynamics to advance knowledge in this area. SNGP provides us with a starting point for the research proposed here.

2.4 Specific Project Objectives and Project Plan

The research will be conducted in the five phases delineated below. The phases and listed objectives are not necessarily sequential. Table 1 shows the timelines for each phase and objective. Milestones are listed in section 2.6.1.

PHASE 1: Building the foundations Project year 1 (09/05-08/06)

- 1.1 A first functional morphology of skeletal elements most involved in flight control and performance will be modeled to determine degree and direction of motion. A sensitivity analysis will take into account the role of cartilage and the stretching abilities of muscles and tendons. This functional morphology may be adapted when results from later phases become available.
- 1.2 The physical structure of the pterosaur wing will be reconstructed. This will involve three basic elements: the bony wing spar, the membranous wing, and the presumably keratinous actinofibrils.
- 1.3 Estimates of the wing area, mass, volume, bone cross sections and other relevant parameters will be derived using the most recent methods and reconstructions. In this study, analogies to birds will be preferred over bats, because pterosaurs are known to have had thin-walled, pneumatic bones in the limbs and girdles, which are lacking in bats.
- 1.4 A three-dimensional geometry of the entire skeleton of *Anhanguera piscator* will be digitized and assembled into a probable articulated structure in SIMM.
- 1.5 A study of the shift from dynamically stable to unstable flight in the evolution of pterodactyls will be started to determine aspects of wing shape and planform that may have been involved in the Cretaceous radiation of these pterosaurs. Emphasis will be placed on changes in proportions among elements of the wing, configurations of the pectoral girdle and deltopectoral crest of the humerus, morphology of the sternum, and the contribution of cranial crests.
- 1.6 Start design flight simulator

PHASE 2: Gliding and soaring flight In project year 2 (09/06-05/07)

- 2.1 The shape of the pterosaur wing, including its posterior attachment (hip, thigh, ankle), and the

- possible membrane between the hind limbs (interfemoral or uropatagial) will be modeled in several ways to determine various effects on flight performance in objective 2.2.
- 2.2 A static aeroelastic analysis will be conducted for the nonlinear pterosaur structure based on a surface panel aerodynamics method, membrane structures theory, and low Reynolds number section analysis. The function of the tail will be assessed.
 - 2.3 Probable representations of major muscle groups with regard to gliding and soaring flight will be created. This study will build on the results of objective 1.1, and will include a sensitivity analysis to determine limits of variability of different models of muscle configuration using the SIMM model described above.
 - 2.4 Flight loads during typical gliding and soaring flights will be estimated and fed into the biomechanics model.
 - 2.5 The actuation potential of the muscle groups determined in objective 2.3 will be estimated based on the flight loads computed in objective 2.4. The corresponding energy expenditure for typical gliding and soaring flight condition will be derived.
 - 2.6 Using the outcomes from objective 2.5, the functional morphology derived in objective 1.1 will be re-evaluated. If necessary, the functional morphology will be re-adjusted and the studies outlined in objectives 2.3 through 2.5 repeated.
 - 2.7 Using outcomes from objectives 2.4 and 2.45 a half-scale mechanical gliding replica will be constructed. Flight tests will be conducted to validate the results of the studies in this phase.
 - 2.8 The computational models developed for the aeroelasticity analysis of gliding and soaring flight will be implemented in the flight simulator.

PHASE 3: Flapping flight

In project year 2 and 3 (06/07 – 08/08)

- 3.1 The aeroelastic analysis will be extended to include quasi-steady flapping motion, illustrating the role of aeroelasticity in achieving efficient, yet passively controlled propulsion through wing flapping.
- 3.2 Probable representations of major muscle groups with regard to flapping flight will be created. This study will build on the results of objective 1.1, and will include a sensitivity analysis to determine limits of variability of different models of muscle configuration using SIMM.
- 3.3 A probable flapping cycle and flight envelope will be designed.
- 3.4 Flight loads during the flapping cycle will be estimated using the analysis of objective 3.1 and fed into the biomechanics model.
- 3.5 The actuation potential of the muscle groups determined in objective 3.2 will be estimated based on the flight loads computed in objective 3.4. The corresponding energy expenditure for the flapping cycle will be derived.
- 3.6 Using outcomes from objective 3.5, the functional morphology will be re-evaluated. If necessary, the functional morphology will be re-adjusted and the studies outlined in objectives 3.2 through 3.5 repeated.
- 3.7 Using outcomes from objectives 3.5 and 3.6, a half-scale mechanical flapping replica will be constructed. Flight tests will be conducted to validate the results of the studies in this phase.
- 3.8 The computational models developed for the aeroelasticity analysis of flapping flight will be implemented in the flight simulator.

PHASE 4: Optimization

In project year 4 (09/08 – 08/09)

- 4.1 Optimal design methods (nonlinear programming with efficient gradient calculations) to determine membrane tension, and applied torsional inputs (through pterosaur musculature) for

- efficient flapping flight will be created. This optimization will be fully integrated with the biomechanics model.
- 4.2 Forward dynamic simulations of flapping motion will be performed and used to evaluate feasibility of various behaviors. Results from the functional morphology studies in phase 3 will be fed into the simulations.
 - 4.3 Using outcomes from objectives 4.1 and 4.2, the functional morphology will be re-evaluated. If necessary, the functional morphology will be re-adjusted.
 - 4.4 Flow computation and visualization tools will be implemented in the flight simulator.
 - 4.5 Using outcomes from objectives 4.1 and 4.2 the half-scale flapping replica will be adjusted and flight tests performed.

PHASE 5: Spin-off and Flight simulation

In project year 4 (09/08 – 08/09)

- 5.1 The effects of scale will be addressed. To this end, models of comparison specimens will be implemented in the aeroelastic and biomechanics models.
- 5.2 Optimization loops will be performed to determine the optimal flight patterns depending on weather conditions and energy requirements. In particular, the optimal gliding flight position, optimal flapping flight sequence and required expenditure for realistic soaring and flapping flight will be determined.
- 5.3 The outcomes of objective 5.2 will be tested using the half-scale mechanical flapping replica.
- 5.4 The graphical simulation tools and research results will be prepared for outreach purposes.

2.5 Prior results from NSF projects

In the past five years, only PI Margot Gerritsen has received NSF funding for high resolution parallel coastal ocean modeling. The relation to the current proposal is indirect. The NSF project involved the design and implementation of a large-scale computational tool for the simulation of coastal ocean flows. Some of the same techniques will be applied in the flow computation and flight simulation part of the current proposal. A project summary is given below.

High Resolution Parallel Coastal Ocean Modeling

PI: Professor R. Street, Department of Civil Engineering
 Co-PIs : Professor O. Fringer, Department of Civil and Environmental Engineering
 Professor M. Gerritsen, Department of Petroleum Engineering
 Funding period: 01/2002-12/2004
 Amount funded: \$482,200

Papers published as a result of this NSF proposal

We currently have four journal papers in preparation. The following papers and abstracts have been published:

- O. B. Fringer, M. Gerritsen, and R. L. Street. "Internal waves in Monterey Bay: An application of SUNTANS", Proc. of the 4th Int. Symposium on Environmental Hydraulics, Hong Kong, 2004.
- Jachec, S., O. Fringer, M. Gerritsen, and R. Street. "SUNTANS on Monterey Bay." 2004 Joint Assembly, Paper: OS33A-05. 2004.
- O. B. Fringer and A. B. Boehm. 2004. "Cross shelf transport induced by internal tides", ASLO/TOS Ocean research conference, Honolulu.

- Jachec, S. "Numerical Modeling of Coastal Ocean Hydrodynamics" Symposium on Current Research in Engineering and Applied Mathematics, Stanford University. 2003.
- O. B. Fringer, M. Gerritsen, S. Jachec, and R. L. Street. 2002. "A new nonhydrostatic parallel coastal ocean model," AGU Fall Meeting, San Francisco, California.
- O. B. Fringer, "Internal wave simulations with SUNTANS", ONR Southwest Regional Review, 2004 Workshop, La Jolla.
- O. B. Fringer and M. Gerritsen, "Nonhydrostatic parallel coastal ocean modeling: SUNTANS", TOMS 2003 Workshop, Boulder.

Outcome of project

The project was highly successful. During project our team developed the SUNTANS (Stanford Unstructured Non-hydrostatic Terrain-following Adaptive Navier-Stokes) solver which is currently being used in many current research projects involving three-dimensional non-hydrostatic flow, including the projects "Secondary Circulation and turbulent mixing in Three Mile Slough" by Profs Fringer and Monismith, and "Cross shelf transport induced by internal tides at Huntington Beach" by Profs Fringer and Boehm at Stanford University. The project was awarded continued funding by the Office of Naval Research in 2004 for a total of \$600,000.

Project summary

SUNTANS is a nonhydrostatic, unstructured-grid, parallel, coastal ocean simulation tool that solves the Navier-Stokes equations under the Boussinesq approximation with a large-eddy simulation of the resolved motions. The formulation is based on the method outlined by Casulli in his 1999 papers, where the free-surface and vertical diffusion are discretized with the theta-method, which eliminates the Courant condition associated with fast free-surface waves and the friction term associated with small vertical grid spacing at the free-surface and bottom boundaries. The grid employs z-levels in the vertical and triangular cells in the planform. Advection of momentum is accomplished with the second-order accurate unstructured-grid scheme of Perot (2000), and scalar advection is accomplished semi-implicitly using the method of Gross (1999), in which continuity of volume and mass are guaranteed when wetting and drying is employed. The wetting and drying capabilities of SUNTANS enable its use for coastal as well as estuarine domains. The theta-method for the free-surface yields a two-dimensional Poisson equation, and the nonhydrostatic pressure is governed by a three-dimensional Poisson equation. These are both solved with the preconditioned conjugate gradient algorithm with diagonal preconditioning. SUNTANS is written in the C programming language, and the message-passing interface (MPI) is employed for use in a distributed memory parallel computing environment. Load balancing and grid-partitioning are being managed with the PARMETIS package.

The grids for SUNTANS are unstructured in the planform and employ z-levels in the vertical. The unstructured grids are generated with the Triangle code of Shewchuck, which computes a Delaunay triangulation. We employ stair-stepped grids in the vertical in order to eliminate errors in computing the baroclinic pressure gradients as well as to enable volume and scalar conservation when computing integrals over each water column. Accurate resolution of complex topography will be accomplished with the use of the immersed boundary method (IBM).

We used SUNTANS to study the formation, propagation and dissipation of high-frequency internal waves in Monterey Bay, CA. Monterey Bay is one of the many coastal regions in the world where a high level of tidal energy dissipation occurs. The causes and origins of this dissipation are still not completely understood. A number of field and modeling studies have been undertaken to observe and predict internal tides and gauge the resulting mixing influence. Large tidal currents tend to lead to increased tidal mixing. However, it is unlikely that interaction with the rough bottom in these areas is the sole cause. Measurements show isopycnals within Monterey Bay can deviate by as much as 60-120 meters in depths ranging from 120-220 meters. This strengthens the argument that another contributor, such as internal

waves (and their breaking), may be a significant contributor to tidal dissipation and resulting increased mixing. We refer to our website <http://suntans.stanford.edu> for more information about this project.

2.6 Contributions to NSF mission and dissemination of research

2.6.1 Scientific journals and conferences

We list anticipated journal publications, as well as the conferences we are planning to present our work.

Article contents	Expected submission date
<i>Journal of Vertebrate Paleontology</i>	
Functional morphology of pterosaurs	April 2006
Pterosaur wing and muscle structure	April 2007
The mechanics of gliding and soaring pterosaur flight	December 2007
The mechanics of flapping pterosaur flight	December 2008
Pterosaur flight simulation	July 2009
<i>Journal of Biomechanics</i>	
Muscle actuation and energy expenditure in gliding and soaring flight	July 2006
Muscle actuation and energy expenditure in flapping flight	July 2007
Dynamic simulation of flapping motion	July 2008
<i>Journal of Aircraft / AIAA Journal</i>	
Nonlinear aeroelasticity analysis of gliding flight	April 2006
Nonlinear aeroelasticity analysis of flapping flight	October 2007
Optimizing flapping flight	April 2008
Simulation of flapping flight	July 2009
<i>Nature</i>	
Agile flyers of the Cretaceous	2008/9

Conference	Attendance
Annual Meeting of the Society of Vertebrate Paleontology	Annually, 2005-2009
International Congress of Vertebrate Morphology	Annually, 2005-2009
Annual AIAA Conference	2006, 2008
American Physical Society – Division of Fluid Dynamics	Annually, 2006-2009
Annual Meeting of the American Society of Biomechanics	Annually, 2006-2008
Congress of the International Society of Biomechanics	2007, 2009

2.6.2 Education

K-12 outreach

The SNGP project had an intense outreach component with a summer program from June to August 2004 for 13 exceptional students chosen from local high schools (San Francisco Chronicle, July 12 2004). The summer program was supported by IISME, the Industry Initiative for Science and Mathematics Education, who financed a high school science teacher to help run the program. The students participated in the project by building a 3m rigid wing glider, the first stage towards the full-scale replica. During this very challenging 8 week-long program, SNGP team members shared knowledge on their fields of expertise, and reviewed the designs proposed by the high school students.

Most of the summer students are eager to continue working on the project as an extra-curricular activity. To satisfy their curiosity, a small reunion is organized once every quarter where the students are given up-to-date progress and background lectures on topics of their choice.



Figure 9. SNGP summer outreach program. left: high school team demonstrating model pterosaur flyers to main design team; center: Team Pterosaur with the 3m flying replica; right: team members manufacturing replica wing

The success and excitement of this program motivates us to continue this summer program in the coming years, and expand it to include K-8 students as well as advanced high school students.

University

This proposal involves three graduate students and a postdoctoral student. SNGP currently has four graduate students involved, a postdoctoral student, and various interns from universities abroad. Professor Ilan Kroo teaches a university course on bio-aerodynamics, which includes pterosaur flight. Professor Gerritsen is a guest lecturer in this popular course. Professor Delp teaches a well-attended course on biomechanics and movement which includes a section on pterosaur flight. Professor Padian teaches vertebrate evolution, including the origin and evolution of flight, in several courses at Berkeley. This integrated study is a unique opportunity to strengthen paleobiology research in the School of Earth Sciences at Stanford through collaborations with the strong paleontology group at UC Berkeley, and the bio-engineering faculty at Stanford.

2.5.3 Outreach to general public

National Geographic, movie and associated national press

The work of the SNGP project will be under the spotlight in a 90-minute National Geographic documentary on pterosaur flight to be released early 2006. This film, the associated national and international publicity, and the national tour planned to advertise the film, will provide unique opportunities to spark new public interest in pterosaurs and pterosaur flight.

Museum exhibit

We hope to create an exhibit on vertebrate flight in general and pterosaur flight in particular suitable for museums such as the National Air Museum and the Smithsonian Institution. This exhibit will include mechanical pterosaur replicas and posters that provide relevant information on paleontology, biomechanics and flight control and performance. Computers will show the biomechanical models and flight simulators, and visitors will be able to run these programs interactively. Information on other vertebrate flyers (birds and bats) and airplane design, both traditional and future, will be included.

Website

The existing website (pterosaur.stanford.edu) would be the gateway for the public to share our advances on solving the mystery of pterosaur flight. It would be linked to knowledgeable sources on vertebrate

evolution, bio-mechanics and animal flight research as well as major museums. Results of this study will be described on web pages of the UC Museum of Paleontology (www.ucmp.berkeley.edu), one of the most authoritative and frequently consulted science education websites in the world.

2.7 Coordination Plan

2.7.1 Key personnel and task assignments

Role	Name	Research areas and supervision	Objectives per PI
PI	Margot Gerritsen	Computational methods, replica design, flight simulator Supervises postdoctoral student Co-supervises PhD student aeroelasticity	1.2, 1.6, 2.2, 2.4, 2.7, 3.1, 3.4, 3.7, 4.1, 4.2, 4.5, 5.1, 5.2, 5.3
co-PI	Kevin Padian	Paleontology, functional morphology Supervises PhD student Co-supervises PhD student biomechanics	1.1, 1.2, 1.3, 1.5, 2.1, 2.3, 2.6, 3.2, 3.6, 4.1, 4.2, 4.3, 5.1, 5.2
co-PI	Scott Delp	Biomechanics, optimization Supervises PhD student Co-supervises postdoctoral student	1.4, 2.3, 2.5, 3.2, 3.5, 4.1, 4.2, 5.1, 5.2
co-PI	Ilan Kroo	Aerodynamics, aeroelasticity, optimization Supervises PhD student	2.1, 2.2, 2.4 3.1, 3.3, 3.4, 4.1, 4.2, 5.1, 5.2
Sub award	Eric Hallberg	Flight simulation, flow computation and visualization Close collaboration with postdoctoral student and PI	1.6, 2.8, 3.8, 4.4, 5.4
Postdoctoral student		Integrated computational and visualization tools, design and implementation of flight simulator, replica design and construction	

2.7.2 Organizational structure

The PI Margot Gerritsen, co-PIs Ilan Kroo and Scott Delp, PhD students B and C, and the postdoctoral student will be located at Stanford University. Co-PI Kevin Padian and PhD student A will be located at UC Berkeley. We expect the communication between the team members to be excellent. There are existing and fruitful collaborations between the PI and co-PIs. Berkeley and Stanford are located very close to each other so that frequent visits between the team members are possible.

Regular weekly meetings will be held in Berkeley and Stanford, and monthly meetings will be organized with the whole project team. Eric Hallberg will spend at least two months per year at Stanford during the summer break to work fulltime on the development of the flight simulator. During the academic sessions, the postdoctoral student will visit Eric Hallberg when necessary.

2.7.3 Milestones

Section 2.4 gives the main and specific objectives of the proposed research. Start and end-dates of the five phases of the project are clearly indicated. Section 2.6.1 gives the anticipated journal articles and conference presentations.