Walking on Water: Biolocomotion at the Interface

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Abstract

We consider the hydrodynamics of creatures capable of sustaining themselves on the
water surface by means other than flotation. Particular attention is given to classifying water walkers according to their principal means of weight support and lateral
propulsion. The various propulsion mechanisms are rationalized through consideration of energetics, hydrodynamic forces applied, or momentum transferred by the
driving stroke. We review previous research in this area and suggest directions for
future work. Special attention is given to introductory discussions of problems not
previously treated in the fluid mechanics literature, with hopes of attracting physicists, applied mathematicians, and engineers to this relatively unexplored area of fluid
mechanics.

1. INTRODUCTION

Walking on water is one of the most striking feats in the natural world. The ability to do so has evolved independently throughout the animal kingdom, among over 1200 species of insects, spiders, birds, fish, reptiles, and mammals (**Figure 1**). Some insects spend their entire lives on the water surface; for other creatures, walking on water is a skill employed sparingly, often to avoid predators. Although various motives for walking on water are mentioned, we focus here on how rather than why creatures do so.

This review is written from the perspective of a fluid mechanician; nevertheless, we hope that it will also be of interest to biologists, particularly to workers in biolocomotion. A thorough discussion of the anatomy, ecology, and evolutionary history of water-walking creatures is beyond the scope and goals of this review. We focus on studies directed toward elucidating the myriad hydrodynamic propulsion mechanisms employed by these creatures. Particular attention is given to rationalizing the ability of creatures to walk on water by identifying the dominant forces employed in weight support and in propelling themselves across the surface. While we do discuss the critical wetting properties of the exterior of some water walkers, we do not consider their internal mechanics; neither do we consider the means of stimulation or control of their movements.

A great deal of work has been directed toward elucidating the propulsion mechanisms of terrestrial creatures, flying birds, and swimming fish, and there have been a number of excellent recent texts devoted to the subject of biolocomotion (Alexander 2002, 2003; Biewener 2003; Denny 1993; Vogel 1994, 2003). Aspects of this literature provide important context for this review, and so are briefly summarized here. Propulsion may be rationalized in terms of force, energy, or momentum transfer between the creature and its surroundings. In order for any creature to move, it must apply a force to its environment; the reaction force then serves to propel it forward. Terrestrial creatures rely on frictional forces between their bodies and land (Dickinson et al. 2000, Radhakrishnan 1998). In the absence of aerodynamic resistance on the walker, one may consider the energy as being transformed between the muscular strain, gravitational potential, and kinetic energies of the creature. When a creature moves through a fluid medium, the kinetic energy of the fluid must also be considered in the energy balance. For some hovering insects, previously shed vortices may be used to generate lift, and so may be considered as an additional energy storage device external to the insect (Dickinson et al. 1999).

Figure 1

Like the ability to fly and swim, walking on water is a skill that has evolved numerous times during the course of evolutionary history. It is used by modern insects, spiders, birds, lizards, and mammals. Water walkers range in size from less than a 1 mm to 3 m, and include (*a*) *Microvelia*, (*b*) *Mesovelia*, (*c*) *Anurida*, (*d*) the fisher spider, (*e*) the basilisk lizard (photo courtesy of Joe McDonald), (*f*) the Western Grebe (photo from the feature film *Winged Migration*), (*g*) man with flotation devices (sketch by Leonardo da Vinci), and (*h*) the tail-walking dolpin (photo courtesy of Fran Hackett, New York Aquarium).
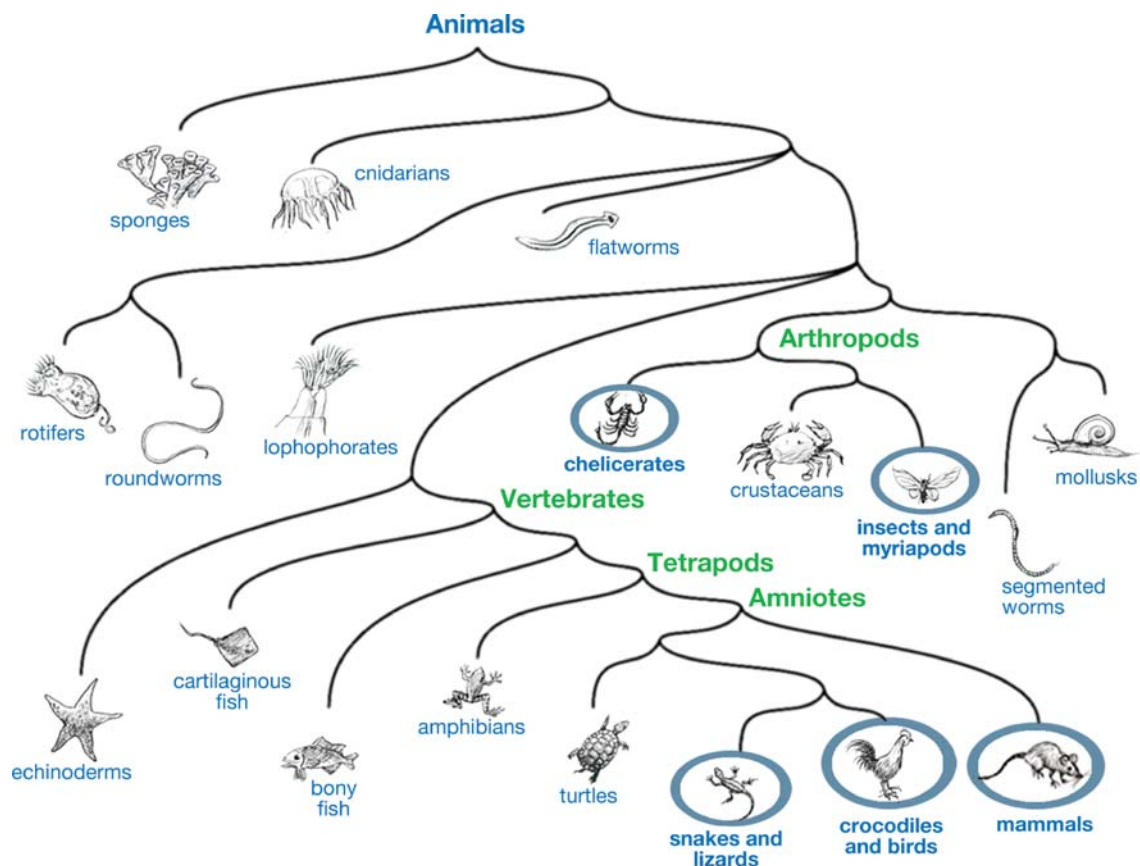
In order to move, swimmers and fliers rely on the hydrodynamic force generated by their driving stroke. The instantaneous hydrodynamic force on a body is simply expressed as the integral of the normal projection of the stress tensor over the body surface. Direct calculation of the hydrodynamic force acting on most creatures is generally impractical, as it requires a precise knowledge of the fluid velocity and pressure fields and the integration of the resulting stresses over the surface of the body over the duration of the driving stroke. It is only for certain forms of geometrically simple propulsion that such a calculation is practical; for example, for the undulatory motion of long, thin swimmers (Lighthill 1970, McHenry et al. 2003, Taylor 1961). For most creatures, the driving stroke is characterized by a complex time-dependent geometry, and a direct computation of the hydrodynamic force is best done numerically. Such has been the approach most commonly taken in recent investigations of fish (Triantafyllou et al. 2000) and insects (Wang 2005); however, simplified two-dimensional geometries are often adopted. An alternative approach to rationalizing the propulsion mechanism of swimmers and fliers involves consideration of the fluid momentum.

The change of momentum of a swimmer or flier generated by its driving stroke is given by the time integral of the hydrodynamic force acting on the body. Provided losses due to viscous dissipation are negligible, conservation of linear momentum requires that the change in momentum of the body be equal to that of the suspending fluid. Consequently, instead of rationalizing the propulsion of a creature by evaluating the hydrodynamic forces acting on it, one may alternatively do so by measuring the net momentum in its fluid wake. Such an approach is most simply applied to creatures whose wakes are characterized by coherent vortical structures, such as the reverse Karman vortex street generated by the carangiform mode of fish swimming (Drucker & Lauder 1999, Triantafyllou et al. 2000) or the vortex rings generated by hovering birds (Kokshaysky 1979; Rayner 1979a,b), octupi, squid, or salps (Linden & Turner 2004). For example, the vertical momentum transfer required for weight support in hovering birds has been considered by Spedding et al. (2003).

The dynamics of propulsion at the air-water surface requires additional consideration of the dynamics of the free surface and the forces generated by its distortion (Baudoin 1955), to be defined in Section 2. The characterization of the dynamics of water-walking creatures thus becomes a complex free-boundary problem, in which aerodynamic, hydrodynamic, and surface forces may act. The energetics are similarly complicated by the presence of the interface, as the gravitational potential and surface energies associated with its distortion must be considered. It is presumably this added degree of dynamical complexity that has discouraged more vigorous work in this area. To date, fluid mechanical studies of water-walking creatures have been largely confined to elucidating the propulsion mechanisms of individual creatures, with particular attention paid to spiders (Section 3.2), the water strider (Section 3.3), and the basilisk lizard (Section 4.2). By reviewing studies of these and other creatures, we here seek to provide an integrative view of water-walking creatures, as well as suggest potentially fruitful directions for future research.

2. FUNDAMENTALS

The propulsion mechanisms of water walkers are as diverse as the creatures themselves. We proceed by categorizing these mechanisms according to the hydrodynamic stresses generated by the driving stroke.

2.1. Dynamics

We consider an arbitrary object striking a free surface (see **Figure 2**). The instantaneous force, **F**, acting on the object may be written precisely as

$$\mathbf{F} = \int_S \mathbf{T} \cdot \mathbf{n} \, dS + \int_C \sigma \mathbf{t} \, d\ell, \tag{1}$$

where S is the area of the body in direct contact with the fluid, and C the line where the free surface separates from the body, specifically, the contact line. $\mathbf{T} = -p\mathbf{I} + 2\mu\mathbf{E}$ is the hydrodynamic stress tensor, p the fluid pressure, μ the dynamic viscosity, and $\mathbf{E} = [\nabla\mathbf{u} + (\nabla\mathbf{u})^T]/2$ the rate of strain tensor. $\mathbf{n}$ and $\mathbf{t}$ are the unit vectors normal and tangent to the free surface. The first term in Equation 1 represents the contribution from the hydrodynamic stress; the second term the force generated by the surface tension. Surface tension is a tensile force per unit length of magnitude σ that acts everywhere tangent to the free surface: Its net contribution is thus prescribed by the line integral in Equation 1.

Application of Stokes theorem allows one to re-express the surface tension force in terms of an integral over the area S:

$$\int_C \sigma \mathbf{t} \, d\ell = \int_S [\sigma (\nabla \cdot \mathbf{n}) \, \mathbf{n} - \nabla\sigma] \, dS. \tag{2}$$

Thus, the net influence of surface tension is to generate a normal stress proportional to σ and the local curvature, $\nabla \cdot \mathbf{n}$, and a tangential stress equal to the local gradient in surface tension, as may arise owing to tangential gradients in temperature or chemical
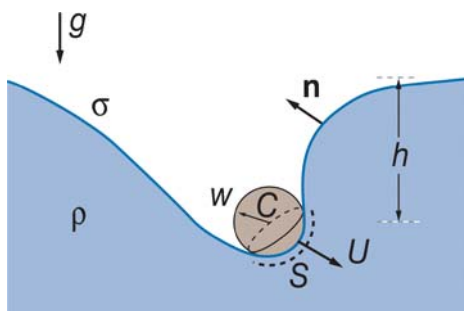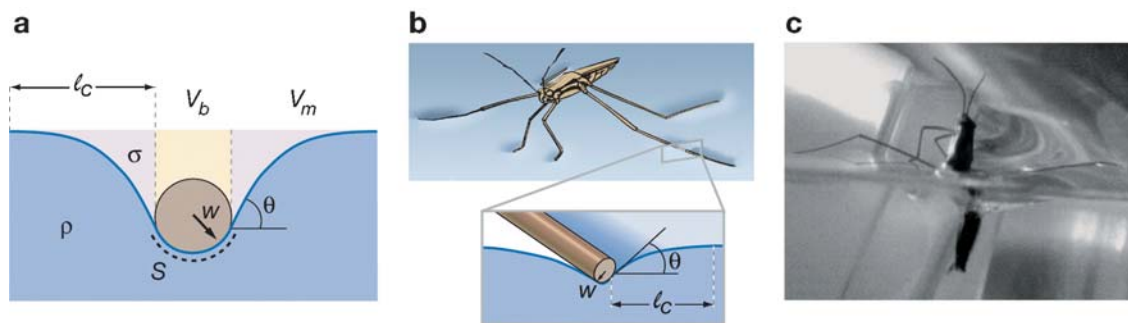

Figure 2

A schematic illustration of the driving leg of a water-walking creature. An object of characteristic size w strikes the free surface at speed U. The surface is characterized by a surface tension σ and its shape by the unit normal **n**. The object's motion will be resisted by some combination of the forces enumerated in Equation 4.

composition (Levich & Krylov 1969). The net surface tension force acting on the body may thus be obtained by integrating the local curvature pressure $\sigma \nabla \cdot \mathbf{n}$ and Marangoni stress $\nabla \sigma$ over its surface.

2.2. Statics

Water-walking creatures are generally more dense than water, and so sink unless sustained by forces capable of bearing their weight. The statics of floating bodies is well understood and may be applied directly in order to understand the vertical force balance on a creature residing at rest on the air-water interface. Consider a body with density greater than that of water $\rho_b > \rho$ and mass M floating at the interface (**Figure 3a**). Its borders are generally adjoined by a meniscus, details of which depend on the wetting properties of the solid (de Gennes et al. 2002), but whose lateral extent corresponds to a capillary length $\ell_c = (\sigma / \rho g)^{1/2} \approx 2.6$ mm. The body weight must be supported by some combination of the buoyancy force, F_b, and curvature force, F_c: $Mg = F_b + F_c$. The buoyancy force is deduced by integrating the hydrostatic pressure $p = \rho g z$ over the body surface S in contact with the water, and so is equal to the weight of fluid V_b displaced above the body and inside the contact line C. The curvature force may be deduced by integrating the curvature pressure over the same area.

Mansfield et al. (1997) and Keller (1998) generalized the Archimedes Principle by demonstrating that the curvature force is precisely equal to the weight of fluid displaced outside the contact line. The buoyancy and curvature forces are thus equal to the weights of the fluid displaced by the meniscus, respectively, in- and out-side the contact line; their relative magnitudes are thus prescribed by the ratio of the characteristic body size w to the capillary length ℓ_c. For creatures with long legs that are thin relative to the capillary length, such as the bulk of water-walking insects, their weight is supported almost exclusively by surface tension (**Figure 3b**).

Figure 3

(*a*) The forces on a floating body. Its weight is supported by a combination of buoyancy and curvature forces, whose magnitudes are given by the weights of the fluid volumes displaced inside and outside its contact line, respectively V_b (yellow) and V_m (pink). (*b*) For a long body thin relative to the capillary length $w \ll \ell_c$, such as the water strider leg, weight is supported principally by the curvature force per unit length $2\sigma \sin\theta$. (*c*) The female water strider penetrates the free surface in order to lay her eggs.

For large bodies, the vertical force is generated primarily by buoyancy: Large bodies more dense than water cannot be sustained by capillary forces and so necessarily sink.

Thus, there is a natural distinction among water-walking creatures according to their principle means of weight support. Creatures small relative to the capillary length, such as water-walking insects (Section 3), rely primarily on surface tension forces for their support: They deform the free surface like a trampoline, thus generating curvature pressures that bear their weight and allow them to rest statically at the free surface. Large creatures (Section 4) cannot reside at rest atop the water: They must strike the free surface with sufficient vigor to generate hydrodynamic forces on their driving legs capable of bearing their weight. Our review considers in turn the dynamics of creatures small and large.
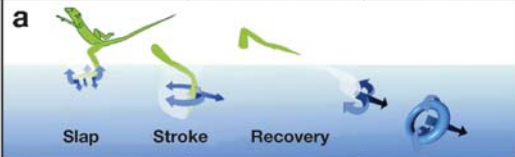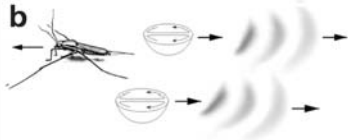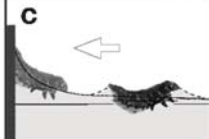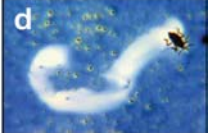
2.3. Dynamic Classification

As we shall see below, the motion of the driving legs of most water walkers is characterized by high Reynolds number. For inviscid flow, the pressure is related to the velocity fields through the unsteady Bernoulli equation, $\frac{\partial \phi}{\partial t} + \frac{1}{2}|\mathbf{u}|^2 + \frac{p}{\rho} - \mathbf{g} \cdot \mathbf{x} = c$. Here $\mathbf{u}$ is the fluid velocity, ϕ the velocity potential, $\mathbf{g}$ gravity, $\mathbf{x}$ the position of the body, and c a constant. Substituting the Bernoulli pressure p into the hydrodynamic stress tensor $\mathbf{T}$, then $\mathbf{T}$ and the curvature force (Equation 2) into Equation 1 yields a net force (Hu 2005; See also D. Hu and J.W.M. Bush. The hydrodynamics of water-walking arthropods. *J. Fluid Mech.* In preparation)

$$\mathbf{F} = \int_S \left[\left(\rho \frac{\partial \phi}{\partial t} + \frac{1}{2}\rho|\mathbf{u}|^2 - \rho\mathbf{g} \cdot \mathbf{x} + \sigma(\nabla \cdot \mathbf{n}) \right) \right] \mathbf{n} - \nabla\sigma \, dA. \qquad (3)$$

The approximate magnitudes of these terms, in addition to the viscous force, may be evaluated in terms of the characteristic leg speed U, the characteristic volume V, area A, and width w of the body in contact with the fluid, and the mean leg depth h below the unperturbed surface height:

$$|\mathbf{F}| \sim \underset{\text{form drag}}{\rho U^2 A} \quad + \quad \underset{\text{buoyancy}}{\rho g h A} \quad + \quad \underset{\text{added mass}}{\rho V \frac{dU}{dt}} \quad + \quad \underset{\text{viscosity}}{\mu U A} \quad + \quad \underset{\text{curvature}}{\sigma \frac{1}{w} A} \quad - \quad \underset{\text{Marangoni}}{\nabla\sigma A},$$

$$(4)$$

where we assume that the local curvature of the meniscus at the area of contact corresponds to the leg width w. The form drag results from the pressure differential generated across the body. If the body strikes the surface asymmetrically, it may utilize the hydrostatic pressure. The added mass force arises from the requirement that fluid be accelerated around an accelerating body; the body's apparent mass increases accordingly (Daniel 1984). The curvature forces are important for water-walking insects: The generation of fore-aft asymmetry in the meniscus of their driving legs plays a critical role in their propulsion (Brocher 1910). Finally, the generation of Marangoni stresses through the release of surface-active fluid is used as an emergency propulsion mechanism by a number of insects (Section 3.5). **Figure 4** represents a categorization of water walkers according to the dominant propulsive forces that they employ.

	Buoyancy	Added mass	Inertia	Curvature	Marangoni
Surface slapping	a (Slap, Stroke, Recovery)				
Rowing and walking			b		
Meniscus climbing				c	
Marangoni propulsion					d

Figure 4

The dynamic classification of water walkers. Large water-walkers, such as the basilisk lizard (*a*), rely on a combination of form drag, added mass, and gravitational forces generated by vigorous slapping of the free surface for both weight support and propulsion. Water-walking insects and spiders rely on surface tension for weight support. Propulsive forces for most insects, such as the water strider (*b*), are generated by some combination of form drag and curvature forces. Others may propel themselves using capillary forces [e.g., (*c*) *Pyrrhalta nymphaeae* larvae] or Marangoni stresses [e.g., (*d*) *Mesovelia*]. **Figure (*a*)** courtesy of Hsieh & Lauder (2004).

Consider the driving leg of a water-walking creature striking the free surface with frequency *f*. The relative magnitudes of the six forces enumerated in Equation 4 are prescribed by five dimensionless groups, the Reynolds *Re*, Weber *We*, Bond *Bo*, Strouhal *St*, and Marangoni *Ma* numbers, defined, respectively, by

$$Re = \frac{Uw}{\nu} = \frac{\text{inertia}}{\text{viscous}} \quad We = \frac{\rho U^2 w}{\sigma} = \frac{\text{inertia}}{\text{curvature}} \quad Bo = \frac{\rho g h}{\sigma/w} = \frac{\text{buoyancy}}{\text{curvature}}$$

$$St = \frac{fw}{U} = \frac{\text{added mass}}{\text{inertia}} \quad Ma = \frac{\nabla \sigma}{\sigma/w} = \frac{\text{Marangoni}}{\text{curvature}}.$$

Assessment of the magnitudes of these dimensionless groups indicates that the great majority of water walkers depend principally on some combination of curvature forces and form drag for their forward propulsion. For water walkers, the treatment of added

mass is complicated by the fact that the driving leg is often accompanied by a volume of air, either a meniscus for water-walking insects and spiders (Section 3), or an air cavity for larger creatures (Section 4). While the resulting added mass may also provide a significant source of thrust for large water walkers ($0.1 < St < 1$), it is negligible for water-walking anthropods ($0.01 < St < 0.1$).

Figure 5 illustrates the dependence of the Bond number on the Weber number for all water-walking creatures for which data was available. Note that there is a natural
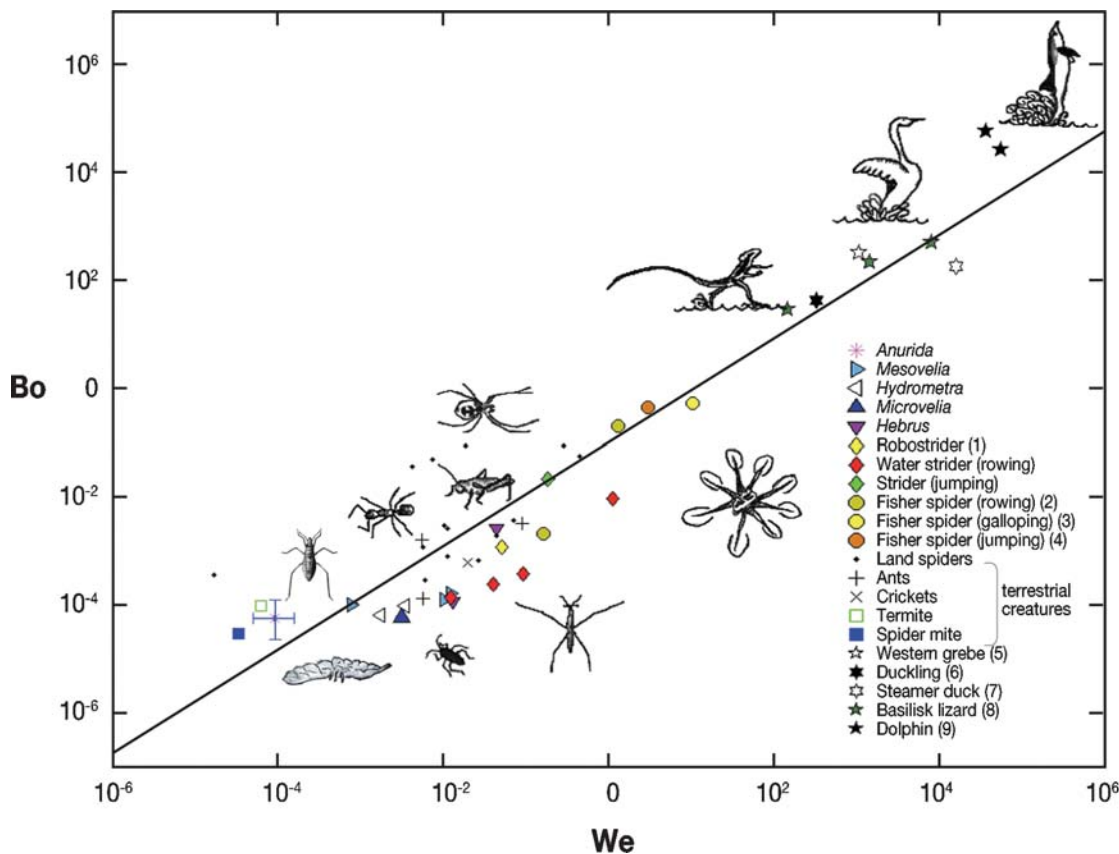
Figure 5

The Bond $Bo = \rho g h w / \sigma$ and Weber $We = \rho U^2 w / \sigma$ numbers for water walkers. Water-walking creatures small relative to the capillary length ($Bo < 1$) are supported by surface tension. Maintenance of the menisci on their driving legs requires that $We < 1$, a criterion satisfied by all water-walking insects apart from the galloping fisher spider. Large water walkers ($Bo \gg 1$) are unconcerned with the effects of surface tension. Note the dependence of the best fit line: $Bo \sim We$. A number of terrestrials capable of walking on water are included. Data for leg width w and speed U collected from: (1) Hu et al. (2003), (2) Suter et al. (1997), (3) Suter & Wildman (1999), (4) Suter & Gruenwald (2000), (5) Nuechterlein & Storer (1982), (6) Aigeldinger & Fish (1995), (7) Livezey & Humphrey (1983), (8) Glasheen & McMahon (1996b), and (9) F. Hacket (personal communication).

division at $Bo = 1$. Small creatures, specifically arthropods, for which $Bo \ll 1$ rely on surface tension for weight support. Their leg speeds are generally characterized by $We < 1$; consequently, their driving legs do not penetrate the free surface. The only arthropod for which $We > 1$ is the fisher spider in its high-speed galloping mode (Suter & Wildman 1999; see Section 3.2). Larger creatures, for which $Bo > 1$, rely on surface tension for neither weight support nor forward propulsion: Their large Weber numbers indicate that their peak leg speeds are unconstrained by surface tension.

Figure 6 illustrates the dependence of the Reynolds number on the Weber number, and illustrates that $0.1 > Re > 10^5$ for all the water walkers examined: The principal hydrodynamic force acting on the driving legs of water walkers is inertial
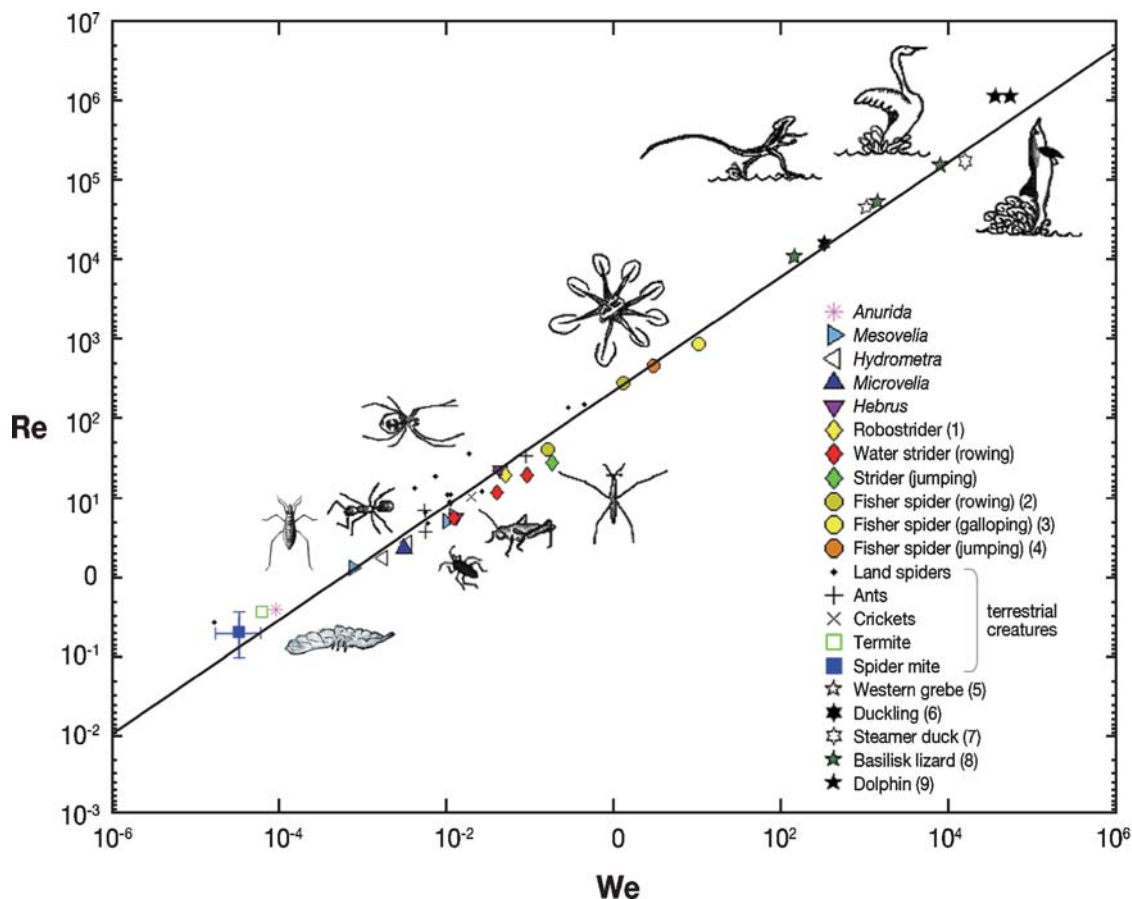
Figure 6

The Reynolds $Re = Uw/\nu$ and Weber $We = \rho U^2 w/\sigma$ numbers for all water walkers. Note the absence of low Re water walkers, and the dependence of the best fit line: $Re \sim We^{3/4}$. Sources of data for species 1–9 are listed in **Figure 5**.

rather than viscous. Finally, we note the dependence of the dimensionless groups $B_o \sim We$, $Re \sim We^{3/4}$ evident in **Figures 5** and **6**, which may be rationalized if the leg speed depends on the leg width as $U \sim w^{1/2}$. Provided body length $L \sim w$ and $h \sim w$, these relations are consistent with Froude's Law of Equivalence of Velocities (Thompson 1961), which relates body speed to body length, $U \sim L^{1/2}$, and is valid for birds and fish. We thus surmise that Froude's Law is also valid for water-walking creatures, presumably because they evolved from terrestrials.

2.4. Wave Drag

The dynamics of all known water walkers is unsteady; nevertheless, it is valuable to briefly review the concept of wave drag, as it has arisen in a number of discussions of water-walking insects. Objects moving steadily at an air-water surface generate surface waves if their speed exceeds the minimum speed of capillary waves, $c_m = 23$ cm/s (Lighthill 1979). The wave field is typically characterized by capillary waves propagating upstream, and gravity waves downstream of the object. The waves radiate energy away from the object, and so represent a source of drag. The ratio of power lost through waves to the steady translation speed U is defined as wave drag. Wave drag is the dominant source of resistance for boats and large ships; indeed, tremendous efforts go into designing hulls that minimize the wave drag (Milgram 1998). Wave drag also plays an important role in limiting the speed for a number of surface swimmers, including ducks (Prange & Schmidt-Nielsen 1970), muskrats (Fish 1982), and rats (Fish & Baudinette 1999).

The wave drag generated by bodies small relative to the capillary length moving at the interface was only recently considered. By generalizing a method developed by Havelock (1966) to describe wave drag associated with gravity waves, Raphael & de Gennes (1995) calculated the power loss to capillary-gravity waves associated with a point pressure distribution moving at an interface. Sun & Keller (2001) extended this study by applying the method of matched asymptotic expansions to calculate the wave drag on a body moving at an interface at large Froude $Fr = U^2/(gL)$ and Weber numbers $We = \rho L U^2 / \sigma$, where U and L are the characteristic speed and length of the body. The result of Raphael & de Gennes (1995) indicates that the ratio of wave to form drag acting on a body moving steadily at a free surface is simply proportional to We^2. The relevance of the concept of wave drag to the unsteady propulsion of water-walking arthropods is considered in Sections 3.2 and 3.3.

3. WATER-WALKING ARTHROPODS

An excellent review of the early works on the biology of water-walking arthropods (insects and spiders) is presented by Hungerford (1919). Water-walking insects were first described during early efforts to classify all animals (Aldrovandi 1618, Ray 1710). The first fundamental studies of surface tension (Plateau 1873) were well cited in the subsequent biology literature, as the critical importance of capillary phenomena on the dynamics and physiological adaptations of water-walking arthropods was quickly recognized (Brocher 1910, Portier 1911). Brocher enumerated

several mechanisms used by semiaquatic creatures to propel themselves along either side of the free surface, or pass from one side to the other. A great compendium of information on the physiology of semiaquatic insects is presented by Andersen (1982).

Baudoin (1955) provides simple scaling arguments that rationalize both upper and lower bounds on water-walking creatures. He defines the margin of safety for water walkers (henceforth the Baudoin number), $Ba = \frac{Mg}{\sigma P}$, as the ratio of weight Mg to the maximum supporting surface tension force σP that can be generated along the contact perimeter P of the legs. He measured the margin of safety for several species of water-walking arthropods and demonstrated that $Ba \sim L^2$, where L is the characteristic insect size, as one expects because $M \sim L^3$ and $P \sim L$. He further stated that the water strider's large margin of safety enables it to leap and perform other feats of surface acrobatics (e.g., Bush 2005, Bush & Hu 2005).

Baudoin further provides a scaling argument that rationalizes a minimum size for water walkers. As for terrestrial creatures (McMahon & Bonner 1985), the characteristic force F a water walker of characteristic length L can produce is proportional to its cross-sectional area: $F \sim L^2$ (Alexander 1985, Wigglesworth 1950). Surface tension forces associated with deforming or crossing the free surface necessarily scale as $F_s \sim \sigma L$. The ratio of available force to curvature force $F/F_s \sim L$ thus decreases with decreasing body size. It follows that there is a critical size below which creatures cannot effectively manipulate the free surface. Baudoin's suggested bound on the size of water walkers is roughly consistent with observations: We are unaware of any reported water walkers with total length less than 0.5 mm. Additional rationale for a minimum size of insects arises from consideration of internal transport requirements; specifically, hydraulic control of the proboscis (Novotny & Wilson 1997), breathing via diffusion, and blood transport via capillaries (Hunter 2003).

3.1. Wetting Properties

The degree of wetting of a solid by a liquid is determined by both the material properties (which prescribe the energetic cost of wetting per unit area) and the topography of the solid surface (de Gennes et al. 2002). Surface roughening has long been used as a means of rendering a solid hydrophobic: By increasing the contact area, one increases the energetic cost of wetting, and so encourages a nonwetting situation. The effective contact angle on a roughened surface is prescribed by Cassie's Law (Bico et al. 2002). The rough texture of surfaces is known to enhance water repellancy in textiles (Bartell et al. 1948), plants, and animals (Cassie & Baxter 1945). The vital role of the wetting properties of water-walking arthropods has long been recognized (Brocher 1910, Imms 1906). The hydrophobic character of most water-walking insects is an important adaptation; otherwise, they would be forced to contend directly with surface tension forces each time their leg crosses the air-water interface. As many such insects weigh no more than 1–10 dynes and have total body perimeter of order 1 cm, crossing the interface would require that they generate forces of order 10–100 times their weight.

A number of water-walking insects are highly nonwetting. Dufour (1833) was the first to highlight the importance of the microstructure of the leg coating for

water-walking insects. Andersen (1976) examined a wide range of semiaquatic bugs under an electron microscope and provided detailed characterizations of their hair cover. He, Cheng (1973), and more recently Gao & Jiang (2004), demonstrated that the water strider leg owes its hydrophobicity to its complex surface cover of hairs coated with water-repellant cuticle wax and contoured with fine fluted nanogrooves. The suggestion that the waterproofing is maintained by secretions from the scent glands (Brinkhurst 1960) has been refuted by Staddon (1972). Suter et al. (2003) examined the wetting properties of 25 species of spiders and found a wide range of both adhesion energies and hair densities.

For virtually all water-walking arthropods, the effective contact angle is sufficiently large that air is trapped by the complex hair layer, providing a thin air cushion, or plastron, between the creature and the water (Crisp 1950). Brocher (1910) reported that a number of insects can cross the water surface by virtue of the plastron adjoining their bodies. Noble-Nesbitt (1963) reported that several seafaring insects glisten when submerged, owing to the plastron that covers their hydrophobic exteriors. The presence of the plastron on the surface of submerged terrestrial spiders (Hebets & Chapman 2000, Rovner 1986) and other aquatic insects (Thorpe 1950) enables them to breathe and to survive for extended periods beneath the free surface.

Other insects have various appendages and body parts that are hydrophilic. Nutman (1941), Baudoin (1955), and Noble-Nesbitt (1963) point out that many water walkers have retractable wetting claws, or ungues, at the ends of their hydrophobic tarsal leg segments that they may use to penetrate or raise the free surface. The resulting ability to raise the free surface is critical in the meniscus climbing to be described in Section 3.4. Janssens (2005) (see also Thibaud 1970) describes the unguis of *Anurida* as a three-sided prism, two sides being hydrophobic and the third hydrophylic, and argued the utility of this arrangement for their dynamic stability.

Wigglesworth (1950), Nutman (1941), Baudoin (1955), and Noble-Nesbitt (1963) report that certain surface-dwelling springtails have a wetting ventral tube vesicle that allows them to locally raise the free surface. The springtail may sit atop the surface like a loaded spring (**Figure 7**): The vertical curvature forces acting on its head and tail
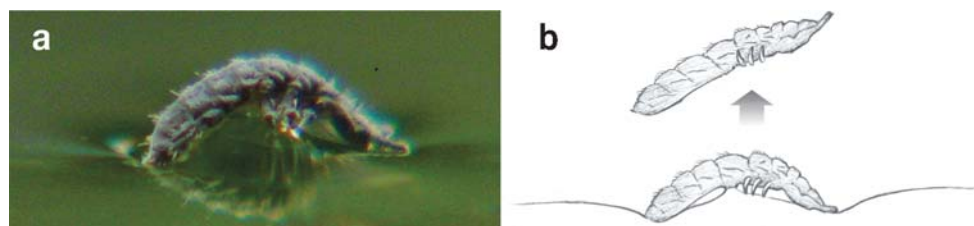
Figure 7

The leaping mechanism of the water-walking springtail. *Anurida* pulls upward on the free surface with its ventral tube, and pushes downward with its nose and tail. Release of the free surface from its ventral tube results in an unbalanced force that launches it upward.

balance its weight in addition to the capillary force generated by its ventral tube. The release of the free surface from the ventral tube results in an unbalanced force that propels it vertically, a technique used to evade aquatic predators. Other adaptations for leaping in the surface-dwelling springtails are discussed by Hopkin (1997).

3.2. Spiders

The water-walking capabilities of spiders are extremely variable (Stratton et al. 2004, Suter et al. 2004). Some have hydrophilic surfaces and so cannot even reside at rest on the water surface. Others have adapted water-walking capabilities for a number of reasons, including foraging on the water surface, the pursuit of mates, evasion of terrestrial predators, and the survival of heavy rains, floods, and falls from trees and ballooning events (Humphrey 1987; Suter 1991, 1992) onto bodies of water. Suter et al. (2003) and Stratton et al. (2004) classified the wettability and water-walking capabilities of 249 species of spiders through a comprehensive cinematographic survey. Hydrophobicity, at least over part of the body, was a necessary prerequisite for water walking. Of the water walkers, the majority propel themselves adequately using their terrestrial gait; however, others have developed a specialized rowing gait (Schultz 1987, Suter et al. 2003). Evaluation of the capabilities of the entire arachnid population lead Stratton et al. (2004) to conclude that the ability to walk on water has evolved several times among spiders and also has been lost on occasion.

Fishing spiders have four distinct modes of navigating the free surface: leaping (Suter & Gruenwald 2000), sailing (Suter & Gruenwald 1999), rowing, and galloping (Gorb & Barth 1994, McAlister 1959, Schultz 1987, Suter 1999). Leaping may be used to ascend menisci or avoid aquatic predators. While Suter & Gruenwald (2000) suggest its relative inefficacy in avoiding predatory fish, Stratton et al. (2004) demonstrates its success in foiling lateral attacks from frogs. As for terrestrial mammals (Hill 1950, Pennycuick 1968), leap height of the fishing spiders was independent of body size (Suter & Gruenwald 2000). Li et al. (2005) developed a numerical model of leaping insects, specifically spring-loaded objects capable of launching themselves vertically from a free surface. Deshefy (1981) first reported the fishing spider's ability to sail across the water surface, and Suter & Gruenwald (1999) experimentally investigated this means of propulsion. By stretching its body into an elevated posture above the free surface, it generates aerodynamic forces that propel it horizontally.

When neither leaping nor sailing, two distinct gaits have been observed for the fisher spider on the free surface. Its relatively casual rowing gait is used in most circumstances; its galloping gait at times when high speeds are required, in prey capture and predator evasion (Gorb & Barth 1994). Suter & Wildman (1999) used high-speed cinematography to show that *Dolomedes* rows at speeds up to 0.2 m/s, but gallops above 0.3 m/s. Suter & Gruenwald (2000) report that rowing speeds are largely independent of body size among fisher spiders varying by a factor of 600 in mass. Suter et al. (1997) and Suter (1999) performed an experimental study of the locomotion of the fisher spider (*Dolomedes triton*). Severed spider legs were emplaced so as to abut the free surface of water in a cylindrical tank. When the tank was

rotated, steady relative motion was generated between the leg and fluid. They argued that, because the spider's leg speed is relatively constant during the driving stroke, a quasi-steady model was appropriate. The authors thus sought to assess the relative magnitudes of wave drag, form drag, and the curvature force on the driving leg of a fisher spider.

Wave drag was eliminated from contention on the grounds that no waves were observed in their experiments below the minimum capillary wave speed c_m, and because spider leg speeds are less than c_m when they row. The curvature force was eliminated from contention on the grounds that the measured force was not greatly influenced by changing the surface tension of the suspending fluid. Force measurements allowed the authors to deduce the dependence of the hydrodynamic force F on flow speed U, surface tension, and leg depth. The authors found that the drag F on the isolated leg was of the form $F \sim U^n$, where $1.6 < n < 2.1$. We note that n being less than 2 is roughly consistent with drag results for flows past flexible bodies (e.g., Alben et al. 2002), and so might be accounted for by consideration of flexure of the spider leg or deformation of the meniscus. The authors conclude that form drag on the driving leg is the primary propulsive force used by spiders. We note that the relative magnitudes of the form drag and curvature forces are roughly prescribed by the Weber number, assessment of which (**Figures 5**, **6**) does support their conclusion for the galloping mode (where the integrity of the meniscus is lost), but suggests that curvature forces are also important during the rowing gait. Finally, the authors note that disturbances observed downstream of the spider leg indicated momentum transfer to the underlying fluid.

A valuable physical picture emerged from the study of Suter et al. (1997): the spiders row, using their legs as oars, and the adjoining menisci as blades. The authors suggest the relevance of this physical picture to a variety of water-walking creatures, including the water strider (Section 3.3). We note that the integrity of the meniscus adjoining the driving leg requires that the curvature pressures be comparable to the dynamic pressures; specifically, $We < 1$. The characteristic $We \sim 10$ of the galloping fisher spider indicates the instability of its menisci: In its galloping gait, the fisher spider's legs protrude through the interface and generate thrust as would bladeless oars. Suter & Wildman (1999) demonstrate that rowing speeds of the fisher spider are limited by both anatomical and hydrodynamical constraints. The spider anatomy enables higher leg tip speeds in the galloping gait; moreover, the integrity of the meniscus vital for efficient rowing is lost at high speeds.

3.3. Water Striders

Water striders are commonly found on ponds, rivers, and the open ocean (**Figure 4b**; Andersen 1976). They are capable of gliding across the water surface or leaping at peak speeds in excess of 130 cm/s; some are capable of winged flight. Their streamlined form suggests the importance of aerodynamic drag in their dynamics. In moderate climates, they range in size from a fraction of a millimeter as hatchlings to a couple of centimeters as adults and weigh 1–10 dynes. In equatorial regions, they may be considerably larger: The largest water strider is the Vietnamese giant, *Gigantometra*

gigas, which may reach a total length in excess of 25 cm (Tseng & Rowe 1999). Their bodies are covered by a thick mat of hair that renders them effectively nonwetting (Andersen 1982, Cheng 1973, Gao & Jiang 2004). Hu et al. (2003) calculate the Baudoin number *Ba* for 253 species of water striders and examine the dependence of body shape on size. Their study indicates that the requirement of static stability on the free surface rationalizes both the maximum size for striders and their variance from isometry: The legs of large water striders are proportionally longer. Hu et al. (2003) calculate the force applied by the driving stroke of the water strider to be of order 50 dynes, which is comparable to the maximum force that can be applied by the driving leg without penetrating the free surface.

Although the bulk of their lives is spent above the free surface, there are two critical stages in the water strider life cycle that may rely on their crossing the interface. Water striders may hatch from eggs laid beneath the free surface, then swim awkwardly toward the free surface. Infants puncture the free surface, perhaps aided by a surfactant coating. Thereafter, the duration of their lives is spent above the free surface, except when the females penetrate the surface to lay eggs (**Figure 3c**). Seafaring water striders *Halobates* (Andersen & Cheng 2004) lay their eggs on floating objects or seabirds (Cheng & Pitman 2002), thus eliminating the need to cross the interface at any stage of the life cycle (Andersen & Polhemus 1976). Cheng (1973) notes that the air layer covering the seafaring water strider makes it strongly buoyant when submerged, thus enabling it to survive violent dunkings by rain, predators, and breaking waves. Walker (1893) and reports that the plastron allows *Halobates* to take evasive action by diving beneath the surface; however, this behavior was not confirmed by Cheng (1973). In any case, the submerged strider must may be rendered bouyant by its plastron, in which case it swims vigorously downward to avoid surfacing.

The first paper dedicated to the locomotion of water striders appeared following the development of high-speed videography. Bowdan (1978) examined limb coordination and gait changes of striders. Darnhofer-Demar's (1969) observations led him to a consistent picture for water strider propulsion mechanism, "when a water strider rows, it deforms the free surface, generating pivots from which it pushes off." However, the dominant force of resistance at the pivot was not identified. In the absence of flow visualization, the only visible manifestation of fluid motion forced by the water strider are the ripples that indicate the field of capillary waves generated by its driving stroke. Andersen (1976) noted the potential importance of wave drag associated with these waves. Denny (1993) noted that if the generation of surface waves was a necessary prerequisite for surface propulsion, infant water striders, whose leg speeds may be less that the critical steady speed (23 cm/s) required to generate waves, should be unable to move. Their ability to do so was subsequently referred to as Denny's Paradox (Suter et al. 1997).

The resolution of Denny's Paradox required the identification of a hydrodynamic force other than wave drag that acts on the driving leg of an infant water strider. The various candidates are presented in Equation 4. Suter et al. (1997) concluded that the force on the leg of a fisher spider may be largely accounted for in terms of form drag, which is present at speeds both above and below c_m. As indicated in **Figure 5**, both form drag and curvature forces resist the driving leg of the water strider; the

relative magnitudes of these forces are prescribed by the Weber number, which is of order 0.1 for the strider, and so suggests the dominance of curvature forces. Hu et al. (2003) revealed that the wake of the water strider is generally characterized by both waves and subsurface hemispherical vortices (**Figure 4*b***). The momentum in the vortices is comparable to that of the strider and greatly exceeds that in the waves. They concluded that the waves were not critical to the propulsion mechanism, but were rather an inevitable biproduct of the driving stroke. The precise partitioning between the momentum transferred in waves and vortices by a point impulse applied at a free surface has been considered by Buhler (manuscript in preparation), who concludes that two thirds should be transferred in vortices, one third in waves. The final word on the resolution of Denny's Paradox comes from Denny (2004) himself.

The physical picture that emerges for the rowing fisher spider and water strider are similar, and likely applies more broadly to many water-walking insects (Suter et al. 1997). The insects strike the surface at a speed such that $We < 1$ in order to maintain the integrity of the meniscus, which serves as the blade on the paddle of the driving leg. The forces acting on the driving leg will then be some combination of the form drag and curvature force, the relative magnitudes of which are prescribed by the Weber number. The maintenance of the meniscus is important because the net force on a steadily moving meniscus is simply the form drag, which is proportional to its exposed area. In the rare instance that the driving stroke is characterized by a $We > 1$, as is the case for the galloping fisher spider, the driving leg penetrates the surface (Suter et al. 1997). While the thin air layer adjoining the leg precludes wetting, the resulting force on the leg is then simply a form drag proportional to the exposed leg area.

3.4. Meniscus Climbing

Although standing bodies of water such as ponds are flat on a human scale, there is significant topography on the scale of millimetric insects. When such insects attempt to move onto land, floating logs, leaves, or emergent vegetation, they must ascend topography in the form of menisci, which appear to them as frictionless mountains. Their ability to do so was a necessary evolutionary adaptation for ancestral water walkers as they began to colonize the water surface (Andersen 1976). Some relatively large water walkers may surmount the menisci using their traditional means of propulsion; for example, the adult fisher spider and water strider may simply leap over menisci. Others cannot, and so have developed a unique means of meniscus climbing. The insects exploit the attractive force between like-signed menisci (Chan et al. 1981, Kralchevsky & Denkov 2001), deforming the free surface in order to generate lateral forces that carry them up the meniscus at high speed. This mode of propulsion was first reported by Baudoin (1955), who correctly identified capillary attraction as the propulsion mechanism. Further qualitative descriptions of meniscus-climbing insects are provided by Andersen (1976) and Miyamoto (1955). Hu & Bush (2005) present the first quantitative treatment of the dynamics of meniscus climbing.

Baudoin (1955) pointed out that meniscus climbing is performed by both wetting and nonwetting creatures. Wetting creatures, such as the *Pyrrhalta nymphaeae* larve, are circumscribed by a contact line; consequently, by arching their backs, they generate menisci and an associated lateral surface force that drives them up the meniscus (**Figure 8a,b**). Their ascent is best rationalized in terms of energetics: if the surface energy they create through arching their backs exceeds the gravitational potential energy gained through their ascent, they will be drawn up the meniscus by capillary

Figure 8

Meniscus climbing insects generate lateral forces by deflecting the free surface. (*a,b*) Wetting insects such as *Pyrrhalta nymphaeae* larvae are circumscribed by a contact line, and so deform the free surface by arching their backs. (*c*) Nonwetting insects such as *Mesovelia* do so by raising the free surface with their ungues. (*d*) The deflection of the free surface is indicated by the shadows cast: upward with the front and hind feet, and downward with the middle pair.
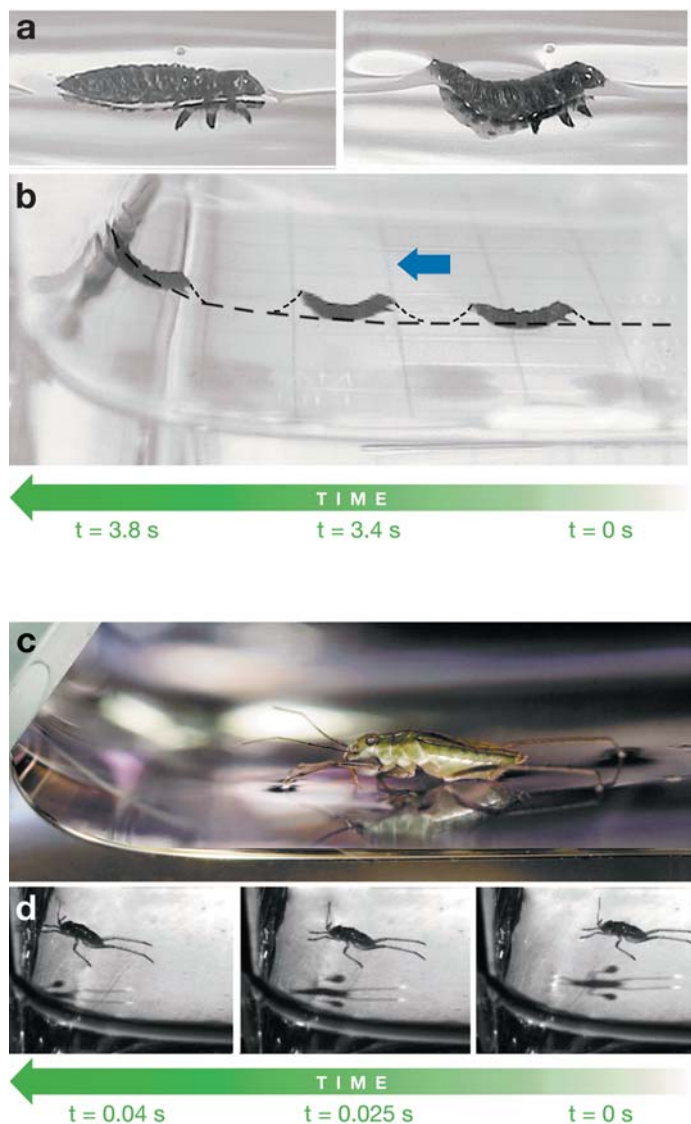
forces (Hu & Bush 2005). Baudoin (1955) performed a simple experiment to demonstrate that floating metal rectangles, when arched slightly, will ascend menisci as do wetting climbers.

The manner in which nonwetting insects deform the free surface is not as obvious; however, as described in Section 3.1, a number have developed specialized feet with retractable hydrophilic claws that allow them to clasp the free surface. **Figure 8c,d** illustrates the posture assumed by *Mesovelia* during the ascent of a meniscus. The insect pulls up with its front legs, thus generating a lateral force that draws it up the meniscus. The torque balance on the insect requires that it pull upward with its hind legs. Finally, the vertical force balance requires that its central pair of legs bear its weight in addition to the vertical forces applied by its front and hind legs. Hu & Bush (2005) applied this simple physical picture to rationalize the ascent rates observed in their experimental study. Both Miyamoto (1955) and Andersen (1976) reported that certain species of insects assume laterally asymmetric, tilted body postures during their ascent of menisci, presumably to maximize the capillary propulsive force.

Finally, we note that capillary attraction is also exploited by some insects, for example *Anurida* (**Figure 1c**), as a means of mutual attraction on flat surfaces. Deforming the interface by assuming the posture indicated in **Figure 7a** enables them to attract others over a distance comparable to a capillary length (approximately their body length) and thus stabilize their colony.

3.5. Marangoni Propulsion

Marangoni flows are those forced by surface tension gradients (Scriven & Sternling 1970). Surfactants, such as common soaps, are molecules that find it energetically favorable to reside at the free surface, and act to decrease the local surface tension. The simplest demonstration of a Marangoni flow is the soap boat (**Figure 9a**). If a small floating object such as a toothpick is placed on a water surface after one end has been dipped in soap, the surface tension at the clean end is greater than at the
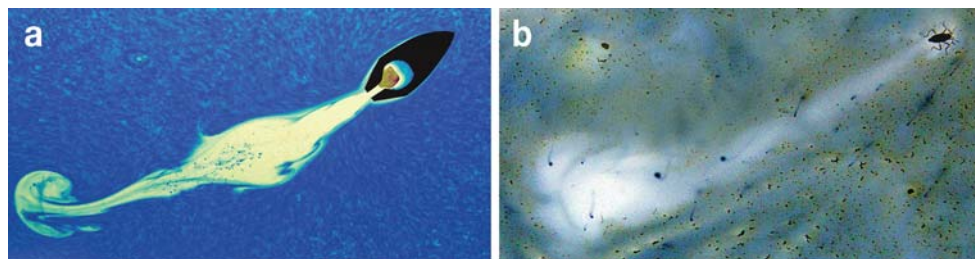
Figure 9

Marangoni propulsion for (*a*) a "soap boat," and (*b*) *Microvelia*. The latter releases a small volume of surfactant; the resulting surface tension gradient propels it forward. In both systems, the surface divergence generated by the surfactant is evident in the clearing of dye from the free surface.

soapy end; consequently, it is propelled away from the soap (e.g., Nakata et al. 2005). A similar principle is employed by a number of water walkers.

Marangoni propulsion was first reported by Billard & Bruyant (1905), who observed its use by a terrestrial insect when it accidentally fell onto the water surface. By releasing a surfactant, it was able to propel itself toward and up the meniscus bordering land and return to its preferred terrestrial environment. Marangoni propulsion by the rove beetle has been reported by Betz (2002), and by semi-aquatic insects, for example *Microvelia* (**Figure 1a**) and *Velia* by Linsenmair & Jander (1976) and Andersen (1976). Schildknecht (1976) and others examined the chemical composition of the rove beetle's secreted surfactant and found it had low solubility in water and reduced the surface tension from 72 to 49 dynes/cm. The authors note the characteristic body postures assumed during Marangoni propulsion. Peak speeds during Marangoni propulsion for *Microvelia* are approximately 17 cm/s, or twice the peak walking speed (Andersen 1982). By dusting the water surface with Lycopodium spores, the authors were able to visualize the path taken by the surfactant ejected. In **Figure 9b**, the surfactant ejected by *Microvelia* clears the initially dyed surface layer. Although the origins of the surfactant are not clear for all creatures, Linsenmair & Jander (1976) note that the fluid in the salivary glands of *Velia* is surface active, and if the rostrum was sealed, no Marangoni propulsion was observed.

Marangoni propulsion by wetting insects is precisely analogous to that of the soap boat: The gradient in the surface tension along the contact line generates a propulsive force. For nonwetting arthropods, the transfer of chemical to kinetic energy is more subtle, as the Marangoni stress must be communicated across the creature's complex surface layer. The body postures assumed and steering method employed during Marangoni propulsion have yet to be rationalized.

4. LARGE WATER WALKERS

4.1. Man

"And when the disciples saw him walking on the sea, they were troubled, saying, It is a spirit; and they cried out for fear."

-Matthew 14:26, King James Version

Barring divine intervention, it is impossible for man to walk on water without the aid of flotation devices, such as those envisaged by Leonardo da Vinci (**Figure 1g**). As we have seen, the vertical force balance on water walkers requires that their weight be supported by either surface tension or inertial forces associated with their feet slapping the surface. A man of mass $M = 70$ kg would require feet of perimeter $P = Mg/\sigma \sim 10$ km to be supported by surface tension. If he relies alternatively on the inertial forces generated by slapping his feet at a mean speed U, he would require feet with area $A = Mg/(\rho U^2)$. Even generous estimates for $U \sim 10$ m/s suggest that the area of a human's feet must be of order 1 m^2 in order for him to walk on water. However, as for all creatures that generate weight support by slapping the surface, thrust generation is not everything: Power generation and stability are

primary concerns. Glasheen & McMahon (1996a) estimate that a human would be able to run on water only if he were able to achieve speeds of order 30 m/s, and to produce 15 times the muscle power available to him.

4.2. Surface Slapping

Small anolis lizards and green iguanas run short distances over water (Hsieh & Lauder 2004); however, only the basilisk lizard (**Figure 1***e*) is capable of walking on water from infancy to adulthood. The basilisk lizard's weight ranges from 2 g as hatchlings to over 500 g as adults. Throughout this size range, they are able to sprint across the water surface at speeds of approximately 1.6 m/s. Although comfortable walking on land or swimming beneath the water surface, they have developed the ability to walk on water to avoid aquatic predators (Rand & Marx 1967).

Glasheen & McMahon (1996a) examined the surface locomotion of the basilisk lizard and elucidated their subtle water-walking technique. The authors character-ized the driving stroke in terms of three distinct phases: slap, stroke, and recovery (**Figure 4***a*). The slapping phase is marked by the vertical impact of their driving foot on the water surface and an associated vertical reaction force. In the stroke phase, their fanned feet generate a deep cavity, against the back of which they push. The associated propulsive force thus results from combined form drag, added mass, and hydrostatic forces. The authors also demonstrate that a critical requirement for their successful surface propulsion is that the lizard be able to retract its foot before the collapse of the air cavity; if not, the resulting downward force on the driving leg will drag it under. While smaller lizards can initiate their water walking from within the water, older, larger, more sluggish lizards must get a running start from land (Rand & Marx 1967). Glasheen & McMahon (1996) rationalized this dependence by consid-ering the lizards' anatomical and kinematic allometry. They predicted that 2-g lizards can generate more than twice the force required for weight support, whereas 200-g lizards can barely support their weight.

The model of Glasheen & McMahon (1996a,b) was based on an accompany-ing series of experiments of vertical impacts of discs on a free surface (Glasheen & McMahon 1996c). Hsieh (2003) notes that the topology of the driving stroke is sig-nificantly more complex and provides a detailed kinematic description thereof. This study was built upon by Hsieh & Lauder (2004), who elucidated the form of the flows generated by the driving stroke through three-dimensional digital particle image velocimetry. Their study demonstrates that substantial weight support is generated during the slap and stroke phases, whereas the principal forward thrust is generated during the stroke phase. Their flow visualization demonstrates that the lizard trans-fers momentum to the underlying fluid in the form of vortex rings that translate backward and downward (**Figure 4***a*).

The dynamics of other large water walkers have received very little attention. The ability of paddling ducklings to avoid wave drag by hydroplaning along the surface has been demonstrated by Aigeldinger & Fish (1995). Various waterfowl can sprint across the surface by vigorous slapping of the surface; some shorebirds do so to prepare for takeoff, using their wings to generate lift as needed. The Western Grebe (**Figure 1***f*)

sprints across water without using its wings as part of its elaborate mating ritual (Nuechterlein & Storer 1982). Steamer ducks propel themselves along the surface by slapping with both their feet and wings (Livezey & Humphrey 1983).

4.3. Tail Walking

If one defines walking on water as propelling oneself at the surface with the bulk of one's body above the water, then the largest water walkers are mammals, specifically dolphins. By vigorously flapping their tails back and forth, dolphins can propel themselves along the free surface with only their tails submerged (Lang 1966; **Figure 1*b***). In general, living creatures can generate forces proportional to their cross-sectional areas, or body size squared, L^2 (Alexander 1985, McMahon & Bonner 1985). To tail walk, a creature must generate a force equal to its weight, which necessarily scales as L^3. As the ratio of force to weight thus scales as $1/L$, one expects tail walking to be easier for smaller swimmers. However, tail walking has only been observed in swimmers with characterisic length of 1–3 m.

Balancing a rod on one's finger can be achieved more easily for long than short rods. Stabilizing a vertical rod by applied vertical or horizontal periodic motions is a generic problem in classical mechanics. For vertical oscillations of a rod of length L with displacement $\gamma \cos \omega t$, the stick is stable when $\omega < (2gL)^{1/2}/\gamma$ (Stephenson 1908). Acheson & Mullin (1993) examined theoretically and experimentally the stability of an inverted pendulum consisting of N rods subjected to vertical forcing at its base. Stability of a rod shaken horizontally requires feedback between the rod and driver, that is, slow variation of the forcing amplitude or frequency; nevertheless, stability is more easily achieved for long rods. By analogy, one expects that stable tail walking is more readily achieved for large swimmers. Thus, one might justify the finite size range of tail-walking creatures: The force balance requires that they be small, whereas stability requires that they be large.

5. DISCUSSION

Our review is confined to a discussion of various modes of propulsion at the interface. Considering the broader role of capillary effects in surface-dwelling arthropods raises countless new questions. For example, both waves and Marangoni effects are used for communication at the free surface. Although generally an inevitable consequence of their motion at the surface, a number of creatures use waves more creatively. The whirligig beetle is preceded by a field of capillary waves that enable it to locate prey via echolocation (Tucker 1969). The fisher spider can detect prey by way of the waves generated by the prey as it struggles to free itself from the interface (Bleckmann 1985). The male water strider generates surface wave signals with frequency 80–90 Hz to identify its sex to prospective partners, thus eliminating the need for visual contact (Stimson Wilcox 1979). Surfactant may also play a role in sexual attraction for certain water-walking arthropods. The male fisher spider finds females by following the pheromone-rich trail left in their wake (Roland & Rovner 1983). Cheng & Roussis (1998) demonstrate that certain male water-walking insects eject a small volume of

lipids containing pheromones that spreads at a characteristic rate of 10 cm/s and serves to attract females. The use of similar chemical signaling in the seafaring water strider has been examined by Tsoukatou et al. (2001), and was proposed as a means by which adults find one another to mate in the open ocean.

Collective motion is also possible at the free surface. Because ants are generally wetting, they struggle to move on the water surface; nevertheless, certain ants have developed a novel means to migrate in times of flood (Tschinkel & Howard 1983). The entire colony flees its mound and binds together in a spherical ball of ants that may be as large as a basketball. The ant ball floats at the surface, partially submerged; however, by maintaining a state of constant motion, the colony generates angular motion of the ball that prevents any of its members from drowning.

As engineers become ever more interested in the manufacture of micro- and nanoscale devices that operate at scales dominated by capillary effects, much may be learned from the natural world. For example, those involved in the design of water-repellant surfaces or submersible water-proof bodies would benefit from careful consideration of the natural coatings of water-walking arthropods (Crisp 1950, Thorpe & Crisp 1949). It is noteworthy that the same physical mechanism employed by meniscus-climbing insects, specifically capillary attraction between floating bodies, has been used to create self-assembling structures on a micro- and nanoscale (Whitesides & Gryzbowski 2002). Biomimetics, the development of machines based on living organisms, may now draw upon new lightweight materials and advances in robotics, and seems poised to move into the world of water walkers. The first waterwalking robots, designed to mimic the water strider (Hu et al. 2003, Sitti 2005), were recently constructed.

It is valuable to place the locomotion of water-walking creatures in context with that of terrestrial creatures, swimmers, and fliers, and so contribute to the emerging integrative view of biolocomotion (Dickinson et al. 1999). First, rationalizing the propulsion of water-walking creatures through consideration of the momentum transferred in their wake was only recently attempted, by Hu et al. (2003) for the water strider and Hsieh & Lauder (2004) for the basilisk lizard (Dickinson 2003). Second, the motion of water walkers is marked by the transfer between strain energies of the creature, kinetic and gravitational energies of the creature and its fluid environment, and the surface energy of the deformed interface. The gravitational potential energy of the deformed interface is used by large water walkers such as the basilisk lizard. The surface energy generated by deforming the free surface is critical in the weight bearing and propulsion of water-walking arthropods. Indeed, quantifying the energy transfer between the creature, fluid, and interface would be an extremely valuable undertaking. It is presumably the complexity of this cycle that makes characterizing the energetics of water-walking creatures more difficult than that of terrestrial creatures, birds, and fish (Rayner 1982, Taylor & Heglund 1982).

Studies of locomotion on land have addressed the issue of stability: For what gaits is a walking animal stable? Studies of land creatures have distinguished between static and dynamic stability (Full et al. 2002). Small insects generally maintain static stability during both standing and walking by keeping their center of mass between their supporting feet. In order to maintain static stability, insects must keep at least

three of their six legs on the ground at all times; it is thus that most hexapod insects use the alternating tripod gait. Larger creatures often have an airborne phase in which they are statically unstable. Small and large creatures alike maintain dynamic stability by pushing, often laterally, with their leg tips (Full et al. 2002). Ting et al. (1994) show that cockroaches utilize both static and dynamic stability. Dynamic stability is often used when the creatures must travel over rough terrain in which footholds are scarce. There has been recent interest in understanding the stability of a creature's propulsion on yielding surfaces such as sand (Kerdok et al. 2002, Lejeune et al. 1998), but little has been done toward characterizing the stability of water-walking creatures. Water-walking insects (e.g., *Microvelia* and *Mesovelia*) generally keep three legs on the water surface at all times in order to maintain static stability. The exception is the water strider, which generally keeps its pairs of front and hind leg tips on the water surface while its middle legs row. The study of Hsieh & Lauder (2004) demonstrated that, as for terrestrial insects and fish, lateral forces generated by the driving stroke may play a critical role in the lizard's stability and maneuverability.

We hope that this review has raised a number of fundamental fluid mechanics problems. Suter et al. (1997) presented the important physical picture of water-walking insects using their menisci as blades. Although one expects the integrity of the meniscus to be maintained provided $We < 1$, it would be valuable to develop a theoretical rationale for the dependence of the hydrodynamic drag on Re and We reported by Suter et al. (1997). While we have here attempted to assess the relative magnitudes of the force components acting on the driving legs of water walkers via simple scaling arguments, the problem is a complex one that deserves more rigorous treatment. How precisely is momentum transferred across the interface, and how are vortices shed by water walkers? It seems clear that the mechanism is quite different for creatures large and small, in the latter case being dominated by surface tension. Is the maneuverability of water walkers influenced by the details of the vortex shedding, as is the case for fish (Triantafyllou et al. 2000)?

Are there really no low Re water walkers; if not, can this absence be rationalized via Baudoin's simple scaling argument? How do the wetting properties of water-walking insects contribute to their life on and beneath the water surface? We have seen that some nonwetting insects are able to survive dunkings by virtue of the thin air layer that accompanies them when they are submerged. Other insects have variable wetting properties that contribute critically to their stability on the surface, or enable them to ascend menisci, or leap vertically off the free surface. Further eliciting the nature of the interaction between the free surface and the hair covering on water-walking arthropods would be of particular interest (Bico et al. 2004, Crisp 1950). Finally, although much work has been done on the static stability of floating bodies (e.g., Erdos et al. 1992), it would be valuable to consider the influence of variable wetting properties on the static and dynamic stability of floating bodies small relative to the capillary length.

The authors hope to have shared their enthusiasm for this exciting field of research, to date left largely unexplored by fluid dynamicists. In addition to providing a review of previous work, we hope to have given some indication of the vast range of fluid mechanics problems arising through the consideration of water-walking creatures.

ACKNOWLEDGMENTS

LITERATURE CITED

Acheson DJ, Mullin T. 1993. Upside-down pendulums. *Nature* 366:215–16

Aigeldinger TL, Fish EF. 1995. Hydroplaning by ducklings: overcoming limitations to swimming at the water surface. *J. Exp. Biol.* 198:1567–74

Alben S, Shelley M, Zhang J. 2002. Drag reduction through self-similar bending of a flexible body. *Nature* 420:479–81

Aldrovandi U. 1618. *Historiam Naturalem de Animalibus Insectis Libri Septem*. Franckfurt: Pauli Jacobi

Alexander RM. 1985. The maximum forces exerted by animals. *J. Exp. Biol.* 115:231–38

Alexander RM. 2002. *Nature's Flyers*. Baltimore, MD: Johns Hopkins Univ. Press

Alexander RM. 2003. *Principles of Animal Locomotion*. Princeton, NJ: Princeton Univ. Press

Andersen NM. 1976. A comparative study of locomotion on the water surface in semiaquatic bugs (Insects, Hemiptera, Gerromorpha). *Vidensk. Meddr. Dan. Naturhist. Foren.* 139:337–96

Andersen NM. 1982. *The Semiaquatic Bugs* (*Hemiptera*, *Gerromorpha*): *Phylogeny*, *Adaptations*, *Biogeography and Classification*. Klampenborg, Den.: Scand. Sci.

Andersen NM. 1995. Fine structure of the body hair layers and morphology of the spiracles of semiaquatic bugs in relation to life on the water surface. *Vidensk. Meddr. Dansk. Naturh. Foren.* 140:7–37

Andersen NM, Cheng L. 2004. The marine insect *Halobates* (Heteroptera: Gerridae): biology, adaptations, distribution, and phylogeny. *Oceanogr. Mar. Biol. Annu. Rev.* 42:119–80

Andersen NM, Polhemus JT. 1976. Water striders (Hemiptera: Gerridae, Vellidae, etc.). In *Marine Insects*, ed. L Chang, pp. 187–224. Amsterdam: North-Holland

Bartell FE, Purcell WR, Dodd CG. 1948. The measurement of effective pore size and of the water-repellency of tightly woven textiles. *Faraday Soc. Disc.* 3:257–64

Baudoin R. 1955. La physico-chimie des surfaces dans la vie des Arthropodes aeriens des miroirs d'eau, des rivages marins et lacustres et de la zone intercotidale. *Bull. Biol. Fr. Belg.* 89:16–164

Betz O. 2002. Performance and adaptive value of tarsal morphology in rove beetles of the genus *Stenus* (Coleoptera, Staphylinidae). *J. Exp. Biol.* 205:1097–113

Bico J, Thiele U, Quéré D. 2002 Wetting of textured surface. *Colloids Surf. A.* 206:41–46

Bico J, Roman B, Moulin L, Boudaoud A. 2004. Elastocapillary coalescence in wet hair. *Nature* 432:690

Biewener AA. 2003. *Animal Locomotion*. Oxford: Oxford Univ. Press

Billard G, Bruylant C. 1905. Sur un mode particulier de locomotion de certains stenus. *C. R. Soc. Biol.* 59:102

Bleckmann H. 1985. Discrimination between prey and non-prey wave signals in the fishing spider *Dolomedes triton* (*Pisauridae*). In *Acoustic and Vibrational Communication in Insects*, ed. K Kalmring, N Elsner, pp. 215–22. Berlin: Paul Parey

Bowdan E. 1978. Walking and rowing in the water strider, *Gerris remigis*. *J. Comp. Physiol.* 123:43–49

Brinkhurst RO. 1960. Studies on the functional morphology of *Gerris najas* DeGeer (Hem. Het. Gerridae). *Proc. Zool. Soc. London* 133:531–39

Brocher F. 1910. Les phénomènes capillaires, leur importance dans la biologie aquatique. *Ann. Biol. Lacustre* 4:89–139

Bush JWM. 2005 Video webpage. **http://www-math.mit.edu/bush/video.htm.**

Bush JWM, Hu DL. 2005. Walking on water. In *Multimedia Fluid Mechanics CD-ROM*, ed. GM Homsy. Cambridge, UK: Cambridge Univ. Press

Cassie ABD, Baxter S. 1945. Large contact angles of plant and animal surfaces. *Nature*. 155:21–22

Chan DYC, Henry JD Jr, White LR. 1981. The interaction of colloidal particles collected at fluid interfaces. *J. Colloid Interface Sci*. 79:410–18

Cheng L. 1973. Marine and freshwater skaters: differences in surface fine structures. *Nature* 242:132–33

Cheng L, Pitman RL. 2002. Mass oviposition and egg development of the ocean skater *Halobates sobrinus* (Heteroptera: Gerridae). *Pacific Sci.* 6(4):441–45

Cheng L, Roussis V. 1998. Sex attractant in the marine insect *Trochopus plumbeus* (Heteroptera: Veliidae): a preliminary report. *Mar. Ecol. Prog. Ser*. 170:283–86

Crisp DJ. 1950. The stability of structures at a fluid interface. *Trans. Faraday Soc*. 46:228–35

Daniel T. 1984. Unsteady aspects of aquatic locomotion. *Am. Zool.* 24:121–34

Darnhofer-Demar B. 1969. Zur Fortbewegung des Wasserläufers *Gerris* lacustris L. auf des Wasseroberfläche. *Zool. Anz. Suppl.* 32:430–39

de Gennes P-G, Quéré D, Brochard-Wyart F, Reisinger A. 2002. *Capillarity and Wetting Phenomena: Drops, Bubbles, Pearls and Waves*. Paris: Springer-Verlag

Denny MW. 1993. *Air and Water: The Biology and Physics of Life's Media*. Princeton: Princeton Univ. Press

Denny MW. 2004. Paradox lost: answers and questions about walking on water. *J. Exp. Biol.* 207:1601–6

Deshefy G. 1981. "Sailing" behaviour in the fishing spider, *Dolomedes triton* (Walckenaer). *Anim. Behav.* 29:965–66

Dickinson MH. 2003. Animal locomotion: how to walk on water. *Nature* 424:621–22

Dickinson MH, Farley CT, Full RJ, Koehl MAR, Kram R, Lehman S. 2000. How animals move: an integrative view. *Science* 288:100–6

Dickinson MH, Lehmann FO, Sane S. 1999. Wing rotation and the aerodynamic basis of insect flight. *Science* 284:1954–60

Drucker EG, Lauder GV. 1999. Locomotor forces on a swimming fish: three-dimensional vortex wake dynamics quantified using digital particle image velocimetry. *J. Exp. Biol.* 202:2393–412

Dufour L. 1833. *Recherches Anatomiques et Physiologiques sur les Hémiptères, Accompagnées de Considèrations Relatives à l'Histoire Naturelle et à la Classification de ces Insectes*, pp. 12, 68–74. Paris: Impr. Bachelier

Erdos P, Schibler G, Herndon RC. 1992. Floating equilibrium of symmetrical objects and the breaking of symmetry. Part 1: prisms. *Am. J. Phys.* 60:335–45

Fish FE. 1982. Aerobic energetics of surface swimming in the muskrat Ondatra zibethicus. *Physiol. Zool.* 55:180–89

Fish FE, Baudinette RV. 1999. Energetics of locomotion by the Australian water rat (*Hydromys chrysogaster*): a comparison of swimming and running in a semi-aquatic mammal. *J. Exp. Biol.* 202:353–63

Full RJ, Kubow T, Schmitt J, Holmes P, Koditschek D. 2002. Quantifying dynamic stability and maneuverability in legged locomotion. *Integr. Comp. Biol.* 42:149–57

Gao XF, Jiang L. 2004. Water-repellant legs of water striders. *Nature* 432:36

Glasheen JW, McMahon TA. 1996a. A hydrodynamic model of locomotion in the basilisk lizard. *Nature* 380:340–42

Glasheen JW, McMahon TA. 1996b. Size dependence of water-running ability in basilisk lizards. *J. Exp. Biol.* 199:2611–18

Glasheen JW, McMahon TA. 1996c. Vertical water entry of disks at low Froude numbers. *Phys. Fluids* 8(8):2078–85

Gorb S, Barth F. 1994. Locomotor behaviour during prey-capture of a fishing spider, *Dolomedes plantarius* (Araneae: Aranidae): galloping and stopping. *J. Arachnol.* 22:89–93

Hebets EA, Chapman RF. 2000. Surviving the flood: plastron respiration in the nontracheate arthropod *Phrynus marginemaculatus* (Amblypygi; Arachnida). *J. Insect Phys.* 46:13–19

Havelock TH. 1966. *Collected Papers of Sir Thomas Havelock on Hydrodynamics*, ed. C Wigley. Washington, DC: Off. Nav. Res.

Hill A. 1950. The dimensions of animals and their muscular dynamics. *Sci. Prog.* 38:209–30

Hopkin SP. 1997. *Biology of the Springtails (Insecta: Collembola)*. Oxford, NY: Oxford Univ. Press

Hsieh ST. 2003. Three-dimensional hindlimb kinematics of water running in the plumed basilisk lizard (*Basiliscus plumifrons*). *J. Exp. Biol.* 206:4363–77

Hsieh ST, Lauder G. 2004. Running on water: three-dimensional force generation by basilisk lizards. *Proc. Natl. Acad. Sci. USA* 101:16784–88

Hu DL. 2005 *The hydrodynamics of water-walking insects*. PhD thesis. Mass. Inst. Tech.

Hu DL, Bush JWM. 2005a. Meniscus-climbing insects. *Nature*. In press

Hu DL, Chan B, Bush JWM. 2003. The hydrodynamics of water strider locomotion. *Nature* 424:663–66

Humphrey J. 1987. Fluid mechanical constraints on spider ballooning. *Oecologia* 73:469–77

Hungerford HB. 1919. The biology and ecology of aquatic semiaquatic Hemiptera. *Kans. Univ. Sci. Bull.* 11:3–328

Hunter P. 2003. Sizing up nature's denizens. *Scientist* 17(19):18–20

Imms AD. 1906. *Anurida (a springtail). LMBC Mem. XIII Typical British Marine Plants and Animals.* London: Williams & Norgate

Janssens F. 2005. *Checklist of the Collembola of the world: note on the morphology and origin of the foot of the Collembola*. **http://www.Collembola.org/publicat/unguis.htm**

Keller J. 1998. Surface tension force on a partly submerged body. *Phys. Fluids* 10:3009–10

Kerdok AE, Biewener AA, McMahon TA, Weyand PG, Herr HM. 2002. Energetics and mechanics of human running on surfaces of different stiffnesses. *J. Appl. Physiol.* 92(2):469–78

Kokshaysky NV. 1979. Tracing the wake of a flying bird. *Nature* 269:146–48

Kralchevsky PA, Denkov DN. 2001. Capillary forces and structuring in layers of colloid particles. *Curr. Opin. Colloid Interface Sci.* 6:383–401

Lang TG. 1966. Hydrodynamic analysis of cetacean performance. In *Whales, Dolphins, and Porpoises*, ed. KS Norris, pp. 410–32. Berkeley, CA: Univ. Calif. Press

Lejeune TM, Willems PA, Heglund NC. 1998. Mechanics and energetics of human locomotion on sand. *J. Exp. Biol.* 201:2071–80

Levich VG, Krylov VS. 1969. Surface-tension-driven phenomena. *Annu. Rev. Fluid Mech.* 1:293–316

Li J, Hesse M, Ziegler J, Woods AW. 2005. An arbitrary Lagrangian Eulerian method for moving-boundary problems and its application to jumping over water. *J. Comput. Phys.* 208:289–314

Lighthill J. 1970. Aquatic animal propulsion of high hydromechanical efficiency. *J. Fluid Mech.* 44:265–301

Lighthill J. 1975. *Mathematical Biofluiddynamics*. Philadelphia: SIAM

Lighthill J. 1979. *Waves in Fluids*. Cambridge, UK: Cambridge Univ. Press

Linden PF, Turner JS. 2004. Optimal vortex rings and aquatic propulsion mechanisms. *Proc. R. Soc. London Ser. B* 271:647–53

Linsenmair K, Jander R. 1976. Das 'entspannungsschwimmen' von *Velia* and *Stenus*. *Naturwissenschaften* 50:231

Livezey BC, Humphrey PS. 1983. Mechanics of steaming in Steamer-ducks. *Auk* 100:485–88

Mansfield EH, Sepangi HR, Eastwood EA. 1997. Equilibrium and mutual attraction or repulsion of objects supported by surface tension. *Philos. Trans. R. Soc. London Ser. A* 355:869–919

McAlister W. 1959. The diving and surface-walking behaviour of *Dolomedes triton sexpunctatus* (Araneae: Pisauridae). *Anim. Behav.* 8:109–11

McHenry MJ, Azizi E, Strother J. 2003. The hydrodynamics of locomotion at intermediate Reynolds numbers: undulatory swimming in ascidian larvae (*Botrylloides* sp.) *J. Exp. Biol.* 206:327–43

McMahon TA, Bonner JT. 1985. *On Size and Life*. New York: Stockholm: Sci. Am. Libr.

Milgram JH. 1998. Fluid mechanics for sailing vessel design. *Annu. Rev. Fluid Mech.* 30:613–13

Miyamoto S. 1955. On a special mode of locomotion utilizing surface tension at the water-edge in some semiaquatic insects. *Kontyû* 23:45–52

Nakata S, Doi Y, Kitahata H. 2005. Synchronized sailing of two camphor boats in polygonal chambers. *J. Phys. Chem. B* 109:1798–802

Noble-Nesbitt J. 1963. Transpiration in *Podura aquatica* L. (Collembola, Isotomidae) and the wetting properties of its cuticle. *J. Exp. Biol.* 40:681–700

Novotny V, Wilson MR. 1997. Why are there no small species among xylem-sucking insects? *Evol. Ecol.* 11:419–37

Nuechterlein GL, Storer RW. 1982. The pair-formation displays of the Western Grebe. *Condor* 84(4):350–69

Nutman S. 1941. The function of the ventral tube in *Onychiurus armatus* (collembola). *Nature* 148:168–69

Pennycuick CJ. 1968. Power requirements for horizontal flight in the pigeon *Columba livia*. *J. Exp. Biol.* 49:509–26

Plateau J. 1873. *Statique Expérimentale et Théorique des Liquides Soumis aux Seules Forces Moléculaires*,Vols. 1, 2. Paris: Gauthier-Villars

Portier P. 1911. Recherches physiologiques sur les insectes aquatiques. *Arch. Zool. Exp. Sér 5* 8:94

Prange HD, Schmidt-Nielsen K. 1970. The metabolic cost of swimming in ducks. *J. Exp. Biol.* 53:763–77

Radhakrishnan V. 1998. Locomotion: dealing with friction. *Proc. Natl. Acad. Sci. USA* 95:5448–55

Rand A, Marx H. 1967. Running speed of the lizard *Basiliscus basiliscus* on water. *Copeia* 1:230–33

Raphael E, deGennes P-G. 1995. Capillary waves caused by a moving disturbance: wave resistance. *Phys. Rev. E* 53(4):3448–55

Ray J. 1710. *Historia Insectorum*, p. 57. London: Impensis/Churchill

Rayner JMV. 1979a. A vortex theory of animal flight. *J. Fluid Mech.* 91:697–63

Rayner JMV. 1979b. A new approach to animal flight mechanics. *J. Exp. Biol.* 80:17–54

Rayner JMV. 1982. Avian flight energetics. *Annu. Rev. Physiol.* 44:109–19

Rayner JMV, Jones G, Thomas A. 1986. Vortex flow visualizations reveal change in upstroke function with flight speed in bats. *Nature* 321:162–64

Roland C, Rovner JS. 1983. Chemical and vibratory communication in the aquatic pisaurid spider *Dolomedes triton* (Araneae, Pisauridae). *J. Arach.* 11:77–85

Rovner JS. 1986. Spider hairiness: Air stores and low activity enhance flooding survival in inland terrestrial species. *Acta X Intl. Congr. Arach. Jaca/Espana* 123–29

Schmidt-Nielsen K. 1984. *Scaling: Why is Animal Size so Important?* Cambridge, UK: Cambridge Univ. Press

Schildknecht H. 1976. Chemical ecology–a chapter of modern natural products chemistry. *Angew. Chem. Int. Ed. Engl.* 15:214–22

Schultz J. 1987. Walking and surface film locomotion in terrestrial and semi-aquatic spiders. *J. Exp. Biol.* 115:427–44

Scriven L, Sternling C. 1970. The Marangoni effect. *Nature* 187:186–88

Sitti M. 2005. **www.me.cmu.edu/faculty1/sitti/nano/projects/waterstrider**.

Spedding G, Rosén M, Hedenstrom A. 2003. A family of vortex wakes generated by a thrush nightingale in free flight in a wind tunnel over its entire natural range of flight speeds. *J. Exp. Biol.* 206:2313–44

Staddon BW. 1972. On the suggestion that the secretion from the methathoracic scent glands of a surface-dwelling aquatic insect, *Gerris najas*, has a waterproofing function. *J. Exp. Biol.* 57:765–69

Stephenson A. 1908. On a new type of dynamical stability. *Mem. Proc. Manch. Lit. Philos. Soc.* 52(8):1–10

Stratton GE, Suter RB, Miller PR. 2004a. Evolution of water surface locomotion by spiders: a comparative approach. *Biol. J. Linn. Soc.* 81:63–78

Stratton GE, Suter RB, Miller PR. 2004b. Taxonomic variation among spiders in the ability to repel water: surface adhesion and hair density. *J. Arach.* 32:11–21

Sun S, Keller J. 2001. Capillary-gravity wave drag. *Phys. Fluids* 13:2416–51

Suter RB. 1991. Ballooning in spiders: results of wind tunnel experiments. *Ethol. Ecol. Evol.* 3:13–25

Suter RB. 1992. Ballooning: data from spiders in freefall indicate the importance of posture. *J. Arachnol.* 20:107–13

Suter RB. 1999. Walking on water. *Am. Sci.* 87:154–59

Suter RB. 2004. Trichobothrial mediation of an aquatic escape response: directional jumps by the fisher spider, *Dolomedes triton*, foil frog attacks. *J. Insect Sci.* 3(19):1–7

Suter RB, Gruenwald J. 1999. Cheap transport for fishing spiders (Araneae, Pisauridae): the physics of sailing on the water surface. *J. Arachnol.* 27:489–96

Suter RB, Gruenwald J. 2000. Predator avoidance on the water surface? Kinematics and efficacy of vertical jumping by *Dolomedes* (Araneae, Pisauridae). *J. Arachnol.* 28:201–10

Suter RB, Rosenberg R, Loeb S, Wildman H, Long JH Jr. 1997. Locomotion on the water surface: propulsive mechanisms of the fisher spider *Dolomedes triton*. *J. Exp. Biol.* 200:2523–38

Suter RB, Stratton G, Miller P. 2003. Water surface locomotion by spiders: distinct gaits in diverse families. *J. Arachnol.* 31:428–32

Suter RB, Wildman H. 1999. Locomotion on the water surface: hydrodynamic constraints on rowing velocity require a gait change. *J. Exp. Biol.* 202:2771–85

Taylor CR, Heglund NC. 1982. Energetics and mechanics of terrestrial locomotion. *Annu. Rev. Physiol.* 44:97–107

Taylor GI. 1961. Analysis of the swimming of long and narrow animals. *Proc. R. Soc. London Ser. A* 214:158–83

Thibaud J-M. 1970. Biologie et écologie des Collemboles Hypogastruidae édaphiques et cavernicoles. *Mém. Mus. Natl. Hist. Nat., Nouvelle Sér. A* 61:83–201

Thompson D. 1961. *On Growth and Form*. Cambridge, UK: Cambridge Univ. Press

Thorpe WH. 1950. Plastron respiration in aquatic insects. *Biol. Rev.* 25:344–90

Thorpe WH, Crisp DJ. 1949. Studies on plastron respiration iv: plastron respiration in the Coleoptera. *J. Exp. Biol.* 25:219–61

Ting LH, Blickhan R, Full RJ. 1994. Dynamic and static stability in hexapedal runners. *J. Exp. Biol.* 197(1):251–69

Triantafyllou MS, Triantafyllou GS, Yue DKP. 2000. Hydrodynamics of fishlike swimming. *Annu. Rev. Fluid Mech.* 32:33–53

Tschinkel WR, Howard DF. 1983. Colony founding by pleometrosis in the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol.* 12:103–13

Tseng M, Rowe L. 1999. Sexual dimorphism and allometry in the giant water strider *Gigantometra gigas*. *Can. J. Zool.* 77:923–29

Tsoukatou M, Cheng L, Vagias C, Roussis V. 2001. Chemical composition and behavioral responses of the marine insect *Halobates hawaiiensis* (Heteroptera; Gerridae). *Z. Naturforsch. Teil C* 56:597–602

Tucker VA. 1969. Wave-making by whirligig beetles (Gyrinidae). *Science* 166:897–99

Vogel S. 1994. *Life in Moving Fluids*. Princeton, NJ: Princeton Univ. Press

Vogel S. 2003. *Comparative Biomechanics*: *Life's Physical World*. Princeton, NJ: Princeton Univ. Press

Walker JJ. 1893. On the genus *Halobates* Esch., and other marine Hemiptera. *Entomol. Mon. Mag.* 29:227–32

Wang ZJ. 2005. Dissecting insect flight. *Annu. Rev. Fluid Mech.* 37:183–210

Whitesides GM, Gryzbowski B. 2002. Self-assembly at all scales. *Science* 295:2418–21

Wigglesworth V. 1950. *The Principles of Insect Physiology*. London: Methuen

Wilcox SR. 1979. Sex discrimination in *Gerris remigis*: role of a surface wave signal. *Science* 206:1325–27