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A10–ECOLOGY AND BIOMECHANICS
Organised by A. Herrel T. Speck for the Biomechanics Group

A10.1 Ecological wood anatomy from a biomechanical perspective

J.S. Sperry (University of Utah)

Wood is a crucial tissue, composing 90% of terrestrial biomass and transporting 50% of terrestrial precipitation back to the atmosphere. Its structure varies tremendously across phylogenetic and functional plant groups, a diversity begging for adaptive explanation. The explanation involves solid- and fluid-mechanics because mechanical support and fluid transport are primary functions of wood. Wood density is a basic trait that determines growth rate and wood strength. A stress analysis yields the surprising result that variation in density may be more related to the mechanical support of the water column, which is under negative pressure, than to support of the tree. Wood conductivity is an equally critical trait because it influences photosynthesis. Analysis of the pit valves between conduits reveals the conflict between conductivity vs. safety from cavitation and mechanical collapse, a trade-off mitigated considerably by the specialized pit anatomy of conifers. Longer and wider conduits can compensate for pit resistance, an advantage exploited by the evolution of vessels. The application of Murray's law to tree hydraulic architecture reveals additional trade-offs that prevent the simultaneous optimization of water transport and biomechanical support in wood structure. This result requires a re-evaluation of Da Vinci's rule for conservation of wood cross sectional area with height and its modern expression in the pipe model. The diversity of wood structure presumably reflects the many different compromises that can be made between support, transport, and economy of construction, with each compromise having advantages unique to a phylogenetic or ecological context.

A10.2 Thigmomorphogenetic acclimation of plants to moderate winds greatly affects height structure in field-gown alfalfa (*Medicago sativa L.*), an indeterminate herb

B. Moulia (UEPF INRA)

Thigmomorphogenesis, the mecanoperceptive control of plant growth, is thought to be involved in the trade-off between light competition and lodging risk, particularly for indeterminate herbs (1). However direct evidences of thigmomorphogenetic reponses to moderate winds in outdoor conditions are scarce, limited to monocots, or to determinate dicots at low densities (2). Field grown alfalfa canopies, an indeterminate dicot, were submitted to three mechanical treatments: supported by frame that reduce stem sway, free standing, and with additional artificial 1 Hz swaying 1 min every hour (Shaked). Wind just above the canopy were recorded by 3D anemometers. The overall wind over the spring experiment was 13 000 km, and only 8000 km in the fall. The turbulence content was unchanged (wind speed cv 0.5) and the wind moderate (< 30 km/h). In spring, the supported canopy was 40% higher than the free standing one, with a large shift in the height distribution of stems, and a large increase in aboveground biomass ($+64\%$), and no change in the number of stems. Additional shaking had no effect, demonstrating effect saturation. On the contrary, in the fall, the supported and free standing treatments had similar height and aboveground biomass, whereas the shaked treatments displayed -36% in height. Thigmomorphogenetic acclimation of plants to moderate winds greatly affects height structure in alfalfa. The biomechanical and ecological aspects of these results are discussed.

(1) Jaffe M. et al. Am. J. Bot. 89 375–382 2002
(2)Crook M.J. and Ennos A.R. Ann. Bot. 77 197–202, 1996

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A 10.3 Drag forces on the southern Bullkelp *Durvillaea* (Phaeophyceae) measured *in situ* and in a flume

D.L. Harder, C.L. Hurd, C.L. Stevens, T. Speck (U. Dunedin & U. Freiburg)

The southern bullkelp *Durvillaea* (Phaeophyceae) is the largest intertidal seaweed. The aim of this study was to identify some of the functional and morphological properties, which allow this species to grow to its enormous size inspite of severe wave exposure. Flow-induced drag forces were measured in a flume on whole thalli of the two sympatric species *D. willana* and *D. antarctica*. The maximum velocity of 2.8 ms^{-1} resulted in drag forces of up to 300 N. A second set of experiments was conducted with transplants of bullkelps and *in situ*. The recorded forces were up to 800 N. Accompanying accelerations at the stipe apex were as high as 54 ms^{-2}. The very flexible lamina reconfigured into a more bundled streamlined shape, reducing the proportional increase of drag with increasing velocity. This effect was significantly higher in individuals with wave-exposed morphology than in individuals with intermediate or wave-sheltered morphology. A simple extrapolation indicates a reduction of drag of up to 75% for velocities of 10 ms^{-1}. It can therefore be concluded that the overall load is effectively minimised through the development of a blade morphology adjusted to the wave exposure and the ability to reconfigure to allow perennial survival in the intertidal ($>$ 9 yrs).

A10.4 Plant cuticles: mechanical properties and functions

Christoph Neinhuis & Hendrik Bargel (T.U. Dresden)

The cuticle serves as the outermost border of plants and represents a composite consisting of three major components: the biopolyester cutin, soluble lipids of various chain lengths (waxes), and cellulose fibres. These fibres tighly connect the cuticle to the cell wall. The cuticle is a multifunctional interface that primarily prevents the plant from uncontrolled water loss, but also serves as a protective layer against biotic and abiotic environmental influences. Representing the outermost structure of a plant, the cuticle may also be of mechanical importance. We investigated tomato fruits and a columnar cactus (*Cereus* spec.). In tomatoes the cuticle has to expand massively without losing its functions. We measured the mechanical properties of enzymatically isolated cuticles in different stages of fruit development. Depending on the cultivar, the stiffness of the cuticle increased in different amounts towards the end of the ripening process while the cell walls of the fruit flesh are softened enzymatically at the same time. Berries are evolved for dispersal, especially by ornithochory. We interprete the cuticle as an mechancially important part to maintain the integrity of the fruit and prevent it from cracking while being picked of the plant.
The cactus shows an amazing influence of water on stiffness and strain of cuticles. While Young's modulus of hydrated cuticles range between 430–480 Mpa (25%, strain), the modulus in dry cuticles goes up to 6500 Mpa (1% strain). These large differences may allow considerable shrinking of the whole plant body during dry season and swelling during rainy season.

A10.5 The importance of flower-pollinator interactions for reproductive isolation and speciation processes in the genus *Salvia*: an experimental approach

M. Reith (U. Freiburg), T. Speck (U. Freiburg), R. Claßen-Bockhoff (U. Mainz), S. Thimm (U. Mainz), E. Tweraser (U. Mainz) and P. Wester (U. Mainz)

The genus *Salvia* is characterised by a 'staminal lever mechanism'. Biomechanical methods and quantitative analyses of the functional morphology were used to test the functioning of the staminal levers and their importance for reproductive isolation among sympatric *Salvia* species. In the first set of experiments, we tested if the forces and energies required to release the staminal levers are relevant for the foraging behaviour of the pollinators. For this purpose, the insects were trained to an 'artificial flower', and the forces exerted by the insects to get to the food source were determined. These forces were then compared to the forces necessary to release the staminal levers, measured with a high-sensitive force test gauge. Our findings show that the staminal levers are evolved for an ease of triggering, and that the forces necessary to release the staminal levers are irrelevant for most insects. In a second set of experiments, the hypothesis is currently tested that the staminal lever mechanism represents a key structure for stabilising sympatric *Salvia* species via accurate and species-specific transfer of pollen on pre-defined regions of the pollinators. We are studying experimentally if the process of pollen deposition on different pollinators is accurate enough to prevent or minimise the transfer of pollen on the stigma of other sympatric *Salvia* species.

A10.6 Xylem water transport failure by cell wall implosion, air-seeding, and membrane rupture in tall Douglas-fir trees

J.-C. DOMEC and B.L. Gartner (Oregon State University)

The cohesion-tension model of water transport states that water is held together by strong internal forces and

that it is pulled through a tree in tension. This tension could cause transport failure in at least three ways: breakage of the tracheid walls (implosion), interruption of the water column with an air bubble namely air-seeding trough pit membrane (margo) pores, or interruption of the water column when a safety features fails—in this case, air seeding when the membrane of an aspirated pit membrane breaks, permitting a gas bubble to spread to another tracheid. Using Douglas-fir trees of two age classes and ranging from 4 to 40 m in height, we asked if there was a constant safety factor with height for any of these three failure modes: implosion, air-seeding and margo breakage. We calculated the safety factor using physiological measurements of vulnerability to embolism, and anatomical measurements of tracheid lumen diameter, cell wall thickness and size of pores and thicknesses of strands in the margos of pit membranes. We showed that on an anatomical basis, as predicted by the 'air-seeding' hypothesis, hydraulic functions are directly linked to bordered pit functioning. This research aimed to elucidate the functional significance of variation in earlywood structure with position in a tree. Increasing tracheid cell wall resistance to implosion by increasing cell wall thickness in earlywood was at the cost of a decreasing resistance to embolism because the torus had to deflect more to be fully aspirated.

A10.7 Ecological Implications of a Biomechanical Novelty: Suction Feeding in Orchid Bees (Apidae: Euglossini)

B.J.B. Borell (University of California, Berkeley)

Energy flux during nectar feeding is optimized at an intermediate sugar concentration, the value of which depends on the morphology of the feeding apparatus and the modality of fluid feeding. Biophysical models predict that a shift from capillary-based lapping to suction feeding will lead to a downward shift in this optimal sugar concentration. Here, I demonstrate that this type of shift has occurred in the orchid bees (Apidae: Euglossini), providing a test of these theoretical predictions. Most bees use a relatively generalized and short proboscis to consume nectar via lapping motions of their hairy 'tongue', but in all four genera of orchid bees the glossa is completely extended and static during feeding. Energy intake optima for orchid bees are similar to those of other suction-feeding insects (30–40% sucrose), whereas optima for bumblebees, honeybees, and stingless bees lie between 50–60% sucrose. Binary choice experiments at automated flowers indicate that orchid bees choose nectars based on viscosity and, consequently, energy intake rate. In nature, orchid bees collect nectars between 34–42% sucrose, which are more dilute than those collected by sympatric bees that lap.

A10.8-Flight mimicry of bees and wasps by foraging hoverflies

Y.C. Golding (University of Manchester); A.R. Ennos (University of Manchester) and M. Edmunds (University of Central Lancashire)

It is generally accepted that many hoverflies (Diptera:Syrphidae) are Batesian mimics of stinging bees and wasps (Hymenoptera). However, though morphological mimicry has been widely studied, less attention has been paid to behavioural mimicry and flight has usually been described only qualitatively. A previous study by us found that the flight behaviour of mimetic droneflies, when foraging, was more similar to that of their honeybee models than to that of other flies. This study aimed to extend this work by quantitatively comparing the flight behaviour of several species of mimetic hoverflies with that of their supposed models, and also some non-mimetic controls. Insects were filmed foraging on arrays of flowers, and flight sequences are currently being analysed to determine flight velocities, deviations from straight line flights and the percentage of time spent hovering. The results of this work will be analysed to determine if these insects do show locomotor mimicry.

A10.9 Structure, performance and adaptive value of mouthpart and tarsus morphology in rove beetles of the genus *Stenus* (Coleoptera, Staphylinidae)

O. Betz (University of Kiel)

The rove beetle genus *Stenus* has experienced a tremendous radiation, comprising $>$ 2100 species widely distributed throughout the world. The evolutionary success of this group of beetles can be partly attributed to specific morphological features: (1) the labium, or lower lip, is modified into a prey-capture apparatus that can be rapidly protruded a long distance out of the body to stick onto elusive and quick-moving prey such as springtails; (2) proceeding from a phylogenetically antecedent condition with slender tarsi, the tarsi of most species are widened and distinctly bilobed, which takes place with a considerable augmentation of tarsal ventral setae. Based on studies on the functional morphology and ultrastructure of these organs, comparative experiments on their performance capacity were carried out to elucidate their adaptive value. Experiments testing the prey-capture success of the labium compared to that of the mandibles suggest that the specialized labial apparatus of *Stenus* beetles provides an ecological advantage in that it permits these predators, in spite of the limited reaction ability and agility of many *Stenus* species, to

catch prey that are capable of sudden and rapid escape behaviour. In terms of the tarsi, the main selective demands driving their widening in several lineages have come from their firm attachment to smooth plant surfaces. This is suggested by measurements of the maximum vertical pulling forces exerted by intact and manipulated individuals on various rough and smooth surfaces. Hence, the evolution of wide tarsi in the various lineages might represent a key innovation that has made possible the expansion of the adaptive zone to live plants.

A10.10 Ecological correlates of acceleration capacity in *Anolis* lizards

B. Vanhooydonck (U. Antwerp) and D.J. Irschick (Tulane University)

Anolis lizards have long served as a textbook example of an adaptive radiation. Species that are morphologically similar occupy similar microhabitats and show similar behaviours (i.e. ecomorphs). Moreover, phylogenetic relationships among *Anolis* species show that each set of ecomorphs has evolved several times independently within the Greater Antilles, making *Anolis* lizards an ideal study system. While in this context sprint speed is probably the best studied locomotor performance trait, others, such as acceleration capacity, have been largely overlooked. This is surprising since anoles, and lizards in general, make use of fast and unpredictable bouts of locomotion when escaping from predators, fighting over territories or capturing prey. Acceleration capacity thus seems ecologically relevant. Additionally, whereas most studies have been limited to microhabitat use, other ecological and behavioural correlates of locomotor performance (e.g. anti-predator behaviour) have not been quantified. In this paper, we test whether interspecific variation in acceleration capacity is correlated to differences in ecology (i.e. microhabitat use and escape behaviour). We compared the locomotor performance and ecology of 16 species of *Anolis* lizards, belonging to three independent radiations (i.e. mainland U.S.A., Jamaica, and Puerto Rico). Acceleration capacity was quantified by means of high speed video recordings (250 Hz) of individual lizards accelerating from a standstill. By subsequent digitization of these video clips, we obtained peak accelerations and velocities for each trial. Both observations on microhabitat use and escape behaviour were done under field conditions. Preliminary data suggest that ecomorphs do differ in acceleration capacity and escape behaviour.

A10.11 The evolution of ecomorphological relationships in the feeding system of labrid fishes

P.C. Wainwright (U. California Davis), M.E. Alfaro (U. California Davis), D.R. Bellwood (James Cook University) and M.W. Westneat (Field Museum Natural History)

Biological diversity is not only about the number of taxa on earth, but also their functional and ecological diversity. My research program is aimed at understanding how functional and ecological diversity arise through studies of the feeding mechanism of fishes. Our recent work on the diversity of jaw linkage mechanics in labrid fishes (wrasses, parrotfish and their kin) using empirical data, mechanical models and simulations of evolution, illustrates what may be two general properties of the origins of high diversity in complex functional systems. First, often a particular functional property can be created by multiple morphologies. Many-to-one mapping provides a mechanism for generating considerable diversity even if lineages are evolving toward distinct adaptive peaks, because selection for a given property can lead to several alternative morphological solutions. To understand how the spectacular functional diversity of labrid fishes has come about we analyzed the degree to which there has been correlated evolution among mechanical properties of the feeding mechanism in 60 labrid fish species. The most striking result from these analyses is that correlations between traits are low (correlations between phylogenetically independent contrasts). Thus, we find that these mechanical properties of the labrid feeding apparatus are not constrained to evolve in concert and this independence has allowed labrids to evolve a remarkable range of mechanical combinations in their feeding mechanisms.

A10.12 Ecological and functional trade-offs of myrmecophagy in lizards

J.J. Meyers (Northern Arizona University), A. Herrel (U. Antwerp) and K.C. Nishikawa (Northern Arizona University)

Myrmecophagy has evolved independently in numerous and diverse lineages, exhibiting many morphological and behavioral modifications that presumably optimize prey uptake and limit energy expenditure. While feeding specializations are reputedly rare in lizards, the North American horned lizards (*Phrynosoma*) and the Australian Thorny Devil (*Moloch horridus*) display morphological convergence in response to their predominate diet of ants. Here we discuss the evolution of the genus *Phrynosoma* by addressing the diet, morphology and performance of the feeding system and comparing those findings with those for its ecological counterpart *M. hor-*

ridus. Although Phrynosoma feed largely on ants, they do not appear to be obligate myrmecophages. The degree of dietary fidelity varies dramatically, with some species focusing on multiple prey types (including beetles). Morphological analysis revealed few head shape differences related to diet, yet morphological estimates and in-vivo bite forces suggest evolution of hard-biting species within *Phrynosoma*. Bite force is inversely related to the number of ants eaten, seemingly constraining poor biters to a restricted diet of softer prey. Feeding kinematics of ant eating are similar in all *Phrynosoma*, displaying a complete lack of processing. However when feeding on harder prey, hard biters perform numerous processing movements. Yet, durophagy is not restricted solely to hard biters, and in at least one species, ant-eating behavior has been co-opted for eating hard prey. The plasticity displayed among *Phrynosoma* is in sharp contrast to the feeding behavior of *M. horridus*, an obligate myrmecophage whose extreme specializations may represent an evolutionary dead end.

A10.13 Feeding behavior, bite force, and the trophic ecology of fruit bats

E.R. Dumont (U. Massachusetts)

Most tropical regions support multi-species assemblages of fruit feeding bats. In many places, bats are the largest component of the frugivore community and play an essential ecological role as seed dispersal agents. Historically, fruit bats were viewed as relatively unspecialized, but closer inspection reveals remarkable morphological diversity in the shape and size of the skull. Along with this diversity, modern field studies demonstrate that most species specialize on a subset of available plant resources. As has been done with other vertebrates, trophic ecology and biomechanics can be linked through data summarizing bite force (feeding performance) and the physical properties of food items. A less well-studied but potentially significant source of variation in bite force production is variation in feeding behavior. Bite force changes with the location of bites along the tooth row (bite points) and behavioral experiments with fruit bats demonstrate that species use predictable, and often unique, combinations of bite points during feeding. Moreover, there are significant differences among species in the plasticity of their behavioral responses to changes in food hardness. For example, many small-bodied species that regularly consume hard fruits exhibit greater behavioral flexibility than soft-fruit feeders or larger bats. Although specific feeding behaviors are associated with different morphological features of the skull in different lineages of fruit bats, the role of feeding behavior in defining trophic niches within assemblages of closely related species should not be overlooked.

A10.14 Functional role of the beak in song production in Darwin's finches: a substrate for ecological speciation?

J. Podos (U. Massachusetts)

Recent studies of vocal mechanics in songbirds have identified a functional role for the beak in sound production. The vocal tract (trachea and beak) filters harmonic overtones from sounds produced by the syrinx, and birds can fine-tune vocal tract resonance properties through changes in beak gape. In this talk I describe beak gape dynamics during song production in seven species of Darwin's finches of the Galápagos Islands, Ecuador. Patterns of gape were analyzed from video sequences taken in the field. Song frequency regressed significantly and positively on beak gape for 38 of 56 individuals, and for all seven species examined. This result provides broad support for a resonance model of vocal tract function in Darwin's finches. Comparison among species revealed significant variation in regression y-intercept values. Body size correlated negatively with y-intercept values, although not at a statistically significant level. Overall these results suggest that patterns of beak use during song production were conserved during the Darwin's finch adaptive radiation, despite the evolution of substantial variation in beak morphology and body size. This study will be discussed in the context of a hypothesis of ecological speciation, which posits that adaptive evolution of beak form and function has led to secondary changes in the acoustic structure of these birds' vocal mating signals.

A10.15 Increased filtration efficiency of attached compared with free-swimming flagellates

K.K. Christensen-Dalsgaard (University of Manchester) and T. Fenchel (University of Copenhagen)

Heterotrophis flagellates are capable of clearing 5–100% of a marine water column for bacteria per day, making them one of the most important components of the microbial food web. They often attach to surfaces while feeding. In the present study, a possible fluid dynamic reason for this attachment in increasing filtration efficiency was investigated theoretically and experimentally. Theoretically, we showed it to be advantageous from a fluid dynamical point of view for cells to be sessile if the radius of the filtration area is smaller than approximately 1.5×cell radius, depending also on the amplitude of the flagellar movement. Experimentally, the effect of attachment on the flow field and clearance of feeding *Paraphysomonas vestita* and *Pteridomonas danica* cells was studied by video microscopy of cells in latex bead suspensions. For attached *P. vestita*

cells, clearance was ca. 70% higher relative to free-swimming cells and for *P. danica* this value was ca. 30%. This is potentially of great ecological importance as it means that the particle content of an aquatic environment must be taken into account when estimating the filtration efficiency of the protozoa. The difference between the two species accords with the fact that *Pteridomonas* sweeps a wider area of the water flow relative to its cell size than *Paraphysomonas*.

A10.16 Morphological and physiological specialisation for digging in amphisbaenians, an ancient lineage of fossorial vertebrates

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Amphisbaenians are legless reptiles that have evolved in isolation from other vertebrate lineages. Most species are predominantly fossorial and use head-first digging to open underground galleries of similar diameter to that of the animal. The purpose of this study was to increase our understanding of the muscle physiology and morphological attributes of digging effort in amphisbaenids. We focus on the Brazilian species *Leposternon microcephalum* (Squamata; Amphisbaenia), a shovel-snouted amphisbaenian that burrows by compressing soil against the upper wall of the tunnel by means of upward strokes of the head. The individuals tested (<72g) exerted pressures on the soil of up to 2.2 kPa. These forces were possible because the fibers of the longissimus dorsi, main muscle associated with burrowing in this species, are highly pennate, thus increasing effective muscle cross-sectional area. Additionally, we found the muscle was characterized by a metabolic transition along its length: proximal, medial and distal fibers are FOG type, but proximal fibers are richer in citrate synthase and more aerobic in nature. This metabolic transition might be related to the heterogeneous power requirements of head-first digging, which are higher at the final step of the compression stroke. Finally, a morphometric model of work requirements shows that, after a given diameter, the work required to compress soil increases exponentially with body diameter. Amphisbaenids, consequently, are constrained to rather small diameters, and therefore increase muscle mass by increasing body length but not body diameter. This hypothesis is compatible with a tendency towards extreme elongation in highly fossorial amphisbaenians.

A10.17-Biomechanics of surface attachment in Asian Weaver ants

W. Federle (U. Wuerzburg)

The capacity of insects to attach to relatively smooth surfaces is a prerequisite for the existence of most insect-plant interactions. Insects on plants must be able to combine firm surface attachment with mobility and manoeuvrability. We use an ant species with extreme attachment performance, the Asian weaver ant (*Oecophylla smaragdina*), as a model to study the mechanisms of surface attachment and locomotion. *Oecophylla* ants need strong adhesive and frictional forces not only during the construction of arboreal leaf nests but also for the capture and transport of very large prey and for the stability of large, hanging aggregations formed to bridge empty spaces between leaves.
The ecology of *Oecophylla* ants has several morphological and biomechanical implications. First, their movable adhesive pads are very large and can resist extreme detachment forces. Based on a combination of active and passive control mechanisms, however, only a fraction of the available contact area is employed during locomotion. Second, the ants' nest construction behaviour requires that individual workers withstand large frictional forces for hours. Despite the presence of an adhesive fluid, the pads of *O.smaragdina* can generate considerable static friction on a smooth substrate. Quantitative estimates of the adhesive film thickness and its viscosity indicate that the assumption of a homogenous film between the pad and the surface is inconsistent with the observed forces and that the rubbery pad cuticle directly interacts with the substrate.

A10.18 Role of the glandular pitcher surface of *Nepenthes ventrata* in insect entrapment

E.V. Gorb (Max-Planck Institute for Metals Research)

In carnivorous plants of the genus *Nepenthes*, specialised trapping organs, pitchers, are composed of several zones serving different functions. To investigate the role of the digestive zone in the trapping mechanism of the pitcher, structural, mechanical, and physico-chemical studies of the glandular surface of the digestive zone were combined with insect behavioural experiments. It is assumed that the contribution of the glandular surface to insect retention differs, depending on insect weight and designs of insect attachment systems. Although the glandular surface is microscopically rough, insects possessing only claws are probably not able to interlock because of surface anisotropy. Stiffness of the pitcher material (Young's modulus: 637.19 ± 213.44 kPa) also does not promote claw clinging. Small insects lacking adhesive pads may use adhesive areas on the glandular

surface, which is inhomogeneous in terms of its adhesive properties, to adhere. Solitary points with very strong adhesion (tenacity: 26–28 kPa) possibly impede insect locomotion. Pad-bearing insects are presumably able to attach to smooth parts of the glandular surface located between glands. High free surface energy (56.84–61.93 mN/m) of the plant substrate may promote adhesion. On the basis of the results of friction experiments with *Calliphora vicina* flies and *Pyrrhocoris apterus* bugs, having pads of two alternative types, it may be concluded that gland secretion decreases the attachment ability in insects with smooth pads but does not influence hairy ones.

A10.19 Structure and biomechanics of hairy attachment systems in insects

S.N. Gorb (Max-Planck Institute for Metals Research)

Many animals bear leg attachment pads with an excellent ability to adhere to a smooth surface as well as to a variety of natural surfaces with rough profiles. There are two alternative designs of such systems: smooth and hairy. The first type of pads, so called smooth systems, such as arolia and euplantulae, occurs in cockroaches, bees, grasshoppers, and bugs. It consists of soft deformable structures with a relatively smooth surface. Pads in representatives of Diptera, Coleoptera, Dermaptera, Megaloptera etc., which appeared convergently in evolution, are covered by relatively long, deformable setae. Using various microscopical techniques (SEM, Cryo-SEM, TEM) and force measurements, we analysed structural and mechanical features of adhesive structures that might be responsible for adhesion enhancement in these systems. We provided experimental evidence of adhesion enhancement by division of contact area. A patterned surface, made out of polyvinylsiloxane (PVS), has a significantly higher tenacity on a glass surface than a smooth sample made out of the same material. Contact splitting leads to the decrease of an effective elastic modulus of the fibre array. This results in adhesion enhancement on smooth and rough substrata. An additional advantage of patterned surfaces is the increased tolerance to defects of individual contacts.

A10.20 Locomotion and predator-prey relationships in fish

P. Domenici (CNR-IAMC Oristano Italy)

Predator-prey interactions include a number of phases, such as search, encounter, attack/escape, capture. Biomechanic (kinematic) studies of fast-start in fish can contribute to our understanding of predator-prey relationships in terms of the processes underlying the attack/escape phase, since most predator-prey encounters in fish are based on fast-start locomotion, both in predator attacks and prey escapes. Many kinematic studies have investigated the locomotor performance of fish during attacks or escape responses, by focusing on distance-derived variables such as cumulative distance, velocity and acceleration, and manoeuvrability variables such as turning radii, turning angles, turning rates. Considerable progress has been made in the last two decades regarding the factors affecting fast-start performance, including the effects of morphology (size and shape) and environmental factors (e.g. temperature, oxygen). Although it has often been assumed that high locomotor performance may confer an advantage in capturing evasive prey or in escaping from predators, these assumptions have rarely been tested. Recent studies trying to correlate swimming performance with escape capabilities suggest that other factors, such as reaction distances, maybe more important than locomotor performance in determining the ability of prey to avoid being captured. Therefore, in order to be ecologically relevant, attack/escape performance studies need to include variables other than locomotion alone, such as reaction distance, response latencies, responsiveness. In addition, the fish's performance during actual predator-prey encounters in nature should be studied in order to evaluate the relative contribution of each performance component to success in capturing prey or escaping from predators.

A10.21 The Mechanics of Human Fingernails

A.R. Ennos, L. Farren and S. Shayler (U. Manchester)

Primates' fingernails are three-layered plates of keratin, which help them grip and manipulate objects. We examined the structure and fracture properties of human fingernails to determine how they resist bending forces while preventing fractures running longitudinally into the nail bed. Nail clippings were first torn manually to examine the preferred crack direction. Next, scissor-cutting tests were performed to compare the fracture toughness of nails in the transverse and longitudinal direction. The fracture toughness of each of the three isolated layers was also measured to determine their relative contributions to the toughness. Finally, the structure was examined using scanning electron microscopy of fracture surfaces and polarized light microscopy of nail sections. When nails were torn, cracks were always diverted transversely, parallel to the free edge of the nail. Cutting tests showed that this occurred because the energy to cut nails transversely, was about half that needed (around 6 kJ m^{-2}) to cut them longitudinally. This anisotropy was imparted by the thick intermediate layer, which was composed of long, narrow cells that are oriented transversely; the energy needed to cut this layer transversely was only a quarter of that needed to cut it longitudinally. In contrast the tile-like cells in the thinner dorsal and ventral layers showed isotropic behaviour. These layers

probably increase the nail's bending strength, and they also wrap around the edge of the nail, so helping to prevent cracks forming.

A10.22 Study of Seasonal fluctuations of an invasive Ctenophore, *Mnemiopsis leidyi* along the Iranian Coast of Caspian Sea surface water

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Following to exotic ctenophore *Mnemiopsis leidyi* invasion of the Caspian sea a series of studies were carried out in order to estimate its importance and its stock assessment in south Caspian sea. The early data show that *M. leidyi* has a vast range of spatio-temporal distribution which vary widely in seasons and stations. The highest biomass observed was 1.5 kg m^{-2} during august–September period. The least biomass has been observed in late February with an average of 20 g m^{-2}. size abundance measurements also show that up to 90% of population have 0–5 mm size. This can be a kind of acclimation to Caspian sea conditions compared to their native area the black sea where the specimen is much bigger or could be a response to living in an oligotrophic sea. Their duration of life was near to 3 months and they have released eggs after one week of birth in 0–5 mm size. Their seasonal biomass and abundances were much bigger in south Caspian coast waters compared to the middle and the north Caspian where other conditions as low salinity and depth could be limiting factors. The vertical distribution data shows also that they are absent below 50 meters or the individuals living there are rare.

A10.23 Morphological and biomechanical correlates of differences in locomotor performance and substrate use in two species of *Anolis* lizards

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Caribbean *Anolis* lizards are well known for their spectacular adaptive radiation in habitat use, performance, and limb shape. Whereas some species such as *Anolis sagrei* live mostly on broad substrates, others such as *Anolis valencienni* utilise mostly narrow substrates. Whereas *A. sagrei* is a much better sprinter on its preferred broad substrate, *A. valencienni* performs relatively well on the narrowest substrates. Here we examine morphological and biomechanical differences between these two species that may underly these differences in performance. Additionally, we examine differences in spatio-temporal gait characteristics that might help explain the observed differences in speed and surefootedness. While running, *A. sagrei* takes large steps at high frequency. *Anolis valencienni*, on the other hand, typically takes shorter steps on all substrates and keeps the limbs closer to the body during the swing phase. Our morphological analysis shows that the pro- and retractors of both limb pairs are much better developed in *A. sagrei*. However, the insertion of the knee flexors in *A. valencienni* is such that they can generate relatively larger torques. Additionally, we observed that *A. valencienni* has a tendinous link between the pelvis and the lower leg, preventing full limb extension during protraction. This likely results in a more stable locomotion on narrow substrates by preventing lateral displacements of the center of mass, away from the substrate.

A10.24 Strike success, kinematics and morphometrics of a dietary specialist and generalist snake, do they differ?

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Species often are categorized as being a generalist (i.e. occupying a broad ecological niche) or a specialist (i.e. occupying a more narrow ecological niche). The 'Principle of Allocation' suggests a trade-off between being a generalist and specialist, i.e. a generalist is expected to be moderately good in exploiting a wide range of resources, whereas a specialist is excellent in exploiting a more narrow range of resources. The underlying idea of this trade-off is that specialisation in function of a certain resource might be disadvantageous for exploiting alternative resources. However, few studies have explicitly tested whether differences in ecological specialisation (niche breadth) are reflected in functional differences. We examined if differences in dietary specialisation between the snake species *Natrix tesselata* and *N. maura* are reflected in differences in functional specialisation (i.e. morphometrics of the feeding system and strike kinematics such as velocity and acceleration), and feeding efficiency (strike success and foraging time). Unexpectedly, we did not find any significant dif-

ference in the variables measured. Probably, the different dietary specialisation between the two snake species is due to divergence in ecology (e.g. prey availability, presence/absence of competitors,…), rather than to different functional specialisations. As ecological specialisation does not necessarily results in functional specialisation as demonstrated here, we would like to advocate investigating specialisation on other levels than ecology to better understand the evolution of ecological specialisation.