Invertebrate paraxial locomotory appendages: design, deformation and control

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Summary

Some principles governing the design of invertebrate paired propulsive appendages are discussed, with particular reference to the extent to which information encoded in their skeletal structure determines their instantaneous shape in locomotion. The hydrostatic paired fins of some cephalopods and marine gastropods, polychaete parapodia and onychophoran lobopodia rely entirely on musculature for shape control. The deformations of walking limbs, though still under muscular control, are strongly influenced by the nature and sequence of movement of the joints. Limbs adapted for walking in air are effectively point-loaded, and their rigid components need to resist axial forces as well as bending and torsional moments. Aquatic walking limbs have little axial loading, while swimming appendages and wings experience only bending and torsional moments, and can exploit these to assist in the deformations that are necessary to gain force asymmetry between half-strokes. Swimming appendages normally employ both muscles and drag, but the wings of insects lack internal muscles, and their changes in shape are largely complex aeroelastic responses to the constantly changing aerodynamic and inertial loads, moderated by muscles inserted at the base. For illustration, wings modelled as thin shells with flexible hinge-lines are used to investigate how transverse distal flexion, essential for controlling the angle of attack in the upstroke, is remotely controlled by the indirect flight muscles.

Key words: annelid, arthropod, cephalopod, pteropod, appendage, limb, wing, walking, swimming, flight, mechanics, locomotion.

Introduction

If an animal is to move relative to its surroundings, it must exert a net force on them and exploit the reaction. It may use its entire body, or part of the body close to its longitudinal axis (axial propulsion), or oscillate projecting appendages (paraxial propulsion) or combine the two. Axial, paraxial and combined propulsion all occur throughout the size range of animals. All three are effective methods for locomotion on or in a substratum and for swimming in water, but flight in air requires paraxial action. Only wings are capable of accelerating enough air to support the weight of an animal as well as to propel it along.

The locomotion of invertebrates has been extensively reviewed by Full (1997). The present paper will deal only with paraxial locomotion, and particularly with some of the mechanical principles that underlie the design of paired appendages. Such appendages are either muscular hydrostats, with or without rigid inclusions, or jointed exoskeletal structures with clearly defined more-or-less rigid components separated by, but often articulating across, areas of flexible cuticle. The former comprise the parapodia of polychaete annelids (Gray, 1939; Mettam, 1967), the fins of cephalopods (Hoar et al., 1994; Packard, 1972) and of some marine gastropods (Farmer, 1970; Satterlie et al., 1985) and the lobopodia of Onychophora (Manton, 1950) and many insect larvae. The latter include the typical legs and swimming paddles of most arthropods (Cannon, 1933; Manton, 1977) and the wings of insects (Wootton, 1981, 1992; Brodsky, 1994).

An animal can elicit propulsive force from its surroundings in two ways: from the elastic reaction of a solid substratum or by accelerating a mass of fluid, opposing its viscosity and inertia. Intermediate conditions exist: walking on a particulate substratum which yields underfoot; or burrowing in waterlogged surroundings, whose effective density and viscosity depend on particle concentration, size and geometry. They will not be discussed here.

Substratum- and fluid-based locomotion create quite different loading patterns on the appendages. Walking limbs are subject to axial forces, usually compressive but sometimes tensile, and to bending and torsional moments. In terms of external forces, the legs of terrestrial walking animals will be effectively point-loaded, and the ground reaction force will have a strong vertical component, supporting the weight. Fluid-dynamic forces at normal walking speeds will be low and, if perceptible, generally adverse. In water, however, a walking animal may be close to neutral buoyancy. Substratum reaction forces will act mainly horizontally, and axial forces...
on the limbs will be relatively low. Drag, however, will be 800 times greater (Martinez et al., 1998) so that the legs will be receiving distributed loads, major bending and perhaps torsional moments. So will burrowing limbs, in both air-filled and water-filled surroundings. Paddles and wings experience only bending and torsion, from fluid-dynamic forces and from inertia, including the often significant inertia of the added mass of fluid moved with the appendages.

Beside these external loads, the internally generated muscular and hydrostatic forces will lead to a complex pattern of local tensile, compressive and shear stresses in the skeleton that are impossible to analyse with any precision.

These factors all influence the design of invertebrate propulsive appendages. The latter need not only to withstand the forces that they experience but also to deform as necessary. Theoretically, this is not essential. Daniel (1984) and Daniel et al. (1992) have shown that the net force gained by accelerating the added mass in a symmetrical rowing stroke could be enough to give a propulsive force, and the filtering limbs of some copepods are known to operate in a transitional Reynolds number range where a small change in stroke velocity can determine whether they act as sieves or as paddles (Cheer and Koehl, 1987; Koehl, 1995). Generally, however, the necessary force asymmetry is achieved by cyclic alteration of the attitude and/or shape of the appendages, involving bending, torsion and changes in exposed surface area.

This account will be concerned principally with propulsive deformation. In particular, it will explore how, and to what extent, information encoded in the skeletal architecture can mediate between the musculature and the inertial and external forces to limit and control this deformation. We shall see how the orientation and form of the joints of arthropod walking limbs both facilitate and restrict their locomotion, how the distributed loads associated with swimming and flying can be enlisted to aid semi-automatic deformation and how automation culminates in the complex, muscle-free wings of pterygote insects.

Substratum locomotion

Terrestrial walking appendages: lobopodia and jointed legs

Walking legs are required to deliver appropriate and appropriately timed forces to the ground, through non-slip tips or elongate tarsi, and to withstand the resulting axial loads and bending moments without rupturing or buckling. The lobopodia of Onychophora, Tardigrada and some insect larvae achieve this effectively as muscular hydrostats, with a thin, flexible cuticle and terminal claws (Manton, 1950). Their short, stout form prevents buckling. Some Cambrian presumed relatives, such as Hallucigenia from the Burgess Shales, seem to have had far more slender lobopodia, but were certainly marine, so that axial forces would have been minimal.

Whereas controlled deformation in lobopodia occurs throughout their length, it is restricted in other terrestrial arthropods to the flexible joints. These are of three main kinds (Fig. 1A–C). Pivot joints have a single degree of rotational freedom. The axis joining the two condyles (points of articulation) crosses the lumen of the tubular appendage, so that antagonistic muscles can pass on either side of it, and the podomeres (the ‘segments’ of the limb) beyond can be both flexed and extended actively. Hinge joints also have one degree of freedom, but lie at the edge of the section, so that they can be flexed, but not actively extended. Monocondylar joints may allow a little anteroposterior rotation as well as flexion, but again no active extension. Within these categories, the field of available movement of any particular joint can be precisely defined by the details of its structure: its orientation in the three planes of space, determining the plane of relative movement of the adjacent podomeres; the amount of play between the condyles, determining how strictly the theoretical degrees of freedom are enforced; and the area and shape of the compliant cuticle, determining the excursion angles permitted either side of the joint (Fig. 1D,E).

The number and sequence of joints down the limb exoskeleton impose the theoretical ultimate limit on its freedom of movement. In life, however, the neuromuscular system will restrict the limb kinematics to a range of meaningful gaits and other movements. Manton (1977) described the type and orientation of joints in sequence along the walking limbs of a wide range of terrestrial arthropods, and Fig. 2 is adapted from a selection of her illustrations. There is considerable variation, but several common features are apparent. Leg promotion and remotion are always facilitated by monocondylar joints or dicondylar pivots, with a nearly
Invertebrate paraxial locomotory appendages

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Vertical axis, near the limb base, permitting the maximum angle of overall swing (although note the scorpion and spider). Horizontal pivots, allowing elevation and depression, are always to be found in the proximal region of the limb. Manton (1977) stressed the need for arthropod legs to flex and extend during the propulsive stroke if the body is to progress in a straight line, and flexion and extension always take place at more distal joints, of all three types. The principal flexion joint should logically be situated approximately half-way down the limb, forming its highest point in the sprawling posture that characterises many land arthropods; in general, this seems to be so.

Fig. 3A is a diagram to illustrate the names of the main podomeres of a leg of a generalised land arthropod. Of those studied by Manton (1977), only insects have pivot joints throughout the pretarsal limb. Diplopoda, Chilopoda, Pauropoda and Symphyla all have only hinge joints beyond the femur, and in Chilopoda the trochanterofemoral joint too is a hinge. Among chelicerates, Limulus, spiders and Opilionida have no pivot joints beyond the femur, and scorpions and Galeodes (Solpugida) have only one.

It follows that, while these arthropods can flex the distal, and usually far longer, regions of their legs, they have no intrinsic muscles that actively extend them. Further, Manton (1977) maintained that, while hydrostatic pressure is capable of extending the legs during the recovery stroke, with the exception of the jumping legs of salticid spiders (Parry and Brown, 1959) it is generally inadequate to do so while they are on the ground. ‘Propulsive extension of these hinge joints is done by the proximal depressor muscles, both intrinsic, near the base of the leg, and extrinsic between the leg and the body, which press the limb-tip firmly on the ground, and with the force from the remotor swing, effect propulsive extension’ (Manton, 1977). In contrast, the pterygote insects have pivots at the femorotibial and tibiotarsal joints. Extensor as well as flexor muscles are present, and the tibia and tarsus can be actively extended. This greatly increases the range of possible movements and the uses to which the legs are put: digging, swimming, jumping, defensive kicking. It may even have assisted in the development of flight, since jumping is a widely employed method of gaining initial flight speed.

In terrestrial locomotion, the legs need to support the weight of the animal as well as to propel it, and the ground reaction has a significant vertical component, giving appreciable axial forces as well as bending moments. The podomeres need to be adapted for rigidity in bending and torsion; they are normally tubular, usually with a circular or slightly elliptical cross section, close to the theoretical optimum for resistance to multidirectional loads. When long, slender and therefore potentially weak, they are almost invariably straight. This not only reduces the probability of buckling in compression (Currey, 1967) but also minimises the likelihood of dangerous torsional moments, which would tend to dislocate and destroy the joints as well as damaging the podomeres themselves.

The diversity of arthropod walking limbs is immense and beyond the scope of this paper. Manton’s (1977) investigations reveal a wide range of morphological adaptations to particular

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**Fig. 3A**

Diagrammatic representation of the sequence of joint types along the walking legs of selected arthropod groups. Modified after Manton (1977). The outer, thicker outlines represent the more proximal podomere, the inner outlines the more distal podomere at each joint. The shaded semicircles represent fixed coxae.

**Fig. 3B**

Diagrams of appendages, illustrating the names of the components. (A) Walking limb of a land arthropod. Note that more podomeres are often present and that the tarsus is often subdivided (see Fig. 2). (B) Parapodium of an errant polychaete annelid.
gaits and locomotory patterns, especially in Onychophora and the myriapod classes. The mechanics of land crab locomotion and of insect walking, running, jumping and pushing have been extensively studied (Delcomyn, 1985; Full et al., 1991; Full and Ahn, 1995; Full and Weinstein, 1992; Evans, 1977; Forsythe, 1991; Bennet-Clark, 1977; Bennet-Clark and Lucey, 1967; Gabriel, 1986; Furth and Suzuki, 1992). Particularly important is the discovery in Blaberus discoidalis (Dictyoptera) that each pair of legs generates its own pattern of ground reaction forces: the first pair tends to decelerate the centre of mass, the third pair to accelerate it, and the second to alternate between the two (Full et al., 1991). This contrasts with vertebrate quadrupeds, in which all legs both accelerate and decelerate the centre of mass, and is likely to be true of many other insects and other arthropod groups with few leg pairs, and even of scutigeromorph centipedes, whose long legs are widely splayed and have very different fields of movement (Manton, 1965, 1977). Also important in the present context, and probably widely applicable, is the realisation that the large ground reaction forces associated with typical arthropod sprawling gaits may help to minimise muscle forces and energy costs by counteracting the large moments of the vertical ground reaction forces about the leg joints (Full et al., 1991). This, in turn, would tend to increase the compression loads in the long tibiae and enhance the need to optimise their section geometry and overall design. These moments and loads would be greatest in the rapid extensions associated with jumping. Alexander (1995) has considered theoretically the optimal design for jumping legs, including those of insects.

The metathoracic legs of locusts beautifully illustrate a range of adaptations associated with jumping: compact coxae; pear-shaped femora containing the pennate jumping muscle appropriate for maximal energy storage in the apodeme and semilunar process; femorotibial pivot joints with an exceptionally large excursion (Heitler, 1977); slender, straight tibiae with an elliptical cross section whose long axis is aligned to minimise bending during the jump; and mobile tibiotarsal joints.

Summarising in the context of this paper, we may note the extent to which the available range of substratum movement of terrestrial arthropods is encoded in the sequence, orientation and detailed design of the joints of the limbs, including the degrees of freedom, the form of the articulation and the angles of excursion in the three dimensions of space. These, in turn, are reflected in the arrangement of the muscles, the space required to house them and the consequent form of the podomeres. The design of both podomeres and joints is further constrained by the need to avoid failure under the axial forces and bending and torsional moments of walking, running and jumping in air.

Walking under water

Aquatic substratum locomotion is found among polychaete annelids and in many arthropods, particularly malacostracan Crustacea, Pycnogonida, insect larvae and water beetles. It has received less attention than has walking in air, and fewer kinematic studies have been published (Mettam, 1967; Pond, 1975; Hui, 1992; Cavanagh and Long, 1994; Jamon and Clarac, 1995, 1997; Domenici et al., 1998; Martinez et al., 1998). The crucial difference lies in the nature of the forces involved. In water, the vertical component of the ground reaction force is proportionally far smaller than in air. If it were wholly absent, purchase would be minimal, and it is no coincidence that habitually walking Crustacea tend to have thick, heavy cuticle reinforced with calcium carbonate rather than adaptations for least weight, as seem general in terrestrial arthropods. Fluid-dynamic forces, however, are many times greater, and the added mass (=virtual mass) of the water moved with the appendages may also be significant. The external loads are therefore distributed along and across the limbs, whose inevitable drag needs to be controlled and appropriately centred.

Annelid parapodia (Fig. 3B) are essentially muscular hydrostats, but they are stiffened by rigid acicula and bear setae. They can act in substratum crawling, or swimming or both, usually assisted in both cases by axial waves (Mettam, 1967; Cavanagh and Long, 1994). In crawling Nereis diversicolor and Nephtys hombergi, there seems little sign of externally driven flexion or torsion. Instead, they achieve force asymmetry by altering the frontal area. The parapodia are extended for the effector stroke by the aciculiferous muscles, the setae are extended by the muscles of the setal sac, and the entire structure is retracted for the recovery stroke (Mettam, 1967). The neuropodial (ventral) acicula and setae of Sphaerosyllis (Manton, 1977) and of most other errant polychaetes grip the substratum when crawling. Polychaete setae vary appreciably in form (Gardiner, 1992) and many appear to be variously adapted for locomotion. Jointed setae occur in several families, the joint being external to the body, with no muscular or nervous control. Merz and Edwards (1998) found in the hesionid Ophiopodromus pugettensis that trimming the setae proximally to the joints affected both crawling and swimming performance more than did more distal trimming, suggesting that passive flexion of the setae plays a role in both forms of locomotion.

While Limulus and the larvae of many insects also walk under water, most aquatic walking arthropods are Crustacea. The walking limbs are the thoracic pereiopods. Like those of chelicerates, myriapods and insects, they are uniramous (unbranched). Most joints are of the pivot type, with flexor and extensor muscles, but with widely varying excursion angles. Two examples illustrate how these operate. Fig. 4 shows semidiagrammatically the joint orientation in a typical leg of Astacus, a freshwater crayfish. The first four podomeres are all situated under the body, and this influences the orientation of their joints. The first post-coxal pivot joint is oblique to the horizontal, allowing elevation/remotion and depression/promotion. The next three are orientated horizontally, but oblique to the limb’s transverse axis: the first and second are somewhat inclined anterodistally and the third postero-distally. Together, these allow elevation and depression of the limb, and their oblique
orientation permits some axial rotation. The fourth joint, between the meropodite and carpodite, is a horizontal pivot, and the principal site of leg retraction. The fifth, between the carpodite and propodite, is again in the vertical plane of the extended leg. Its flexion is limited and asymmetrical, flexing further anteromesally than posterodistally. The most distal joint, to the short claw-like dactylopodite, is another horizontal pivot, with little lateral play in the chelate first two legs, and rather more in the non-chelate third and fourth pairs.

Locomotion has been studied in the related Austropotamobius pallipes (Pond, 1975) and extensively in Procambarus clarkii (Jamon and Clarac, 1995, 1997; Domenici et al., 1998), and I have myself observed Pacifastacus leniusculus. As in Blaberus, the various leg pairs operate very differently. In Pacifastacus walking forward on a level substratum, the two most anterior legs, posterior to the chelipeds, are directed anteriorly and operate by retraction, so pulling the animal forward. As the direction of leg retraction is aligned with the axis of the carpodite/propodite pivot, these two podomeres operate as one, with no mutual bending in the power stroke. The third legs project laterally and operate like the mesothoracic legs of insects, first pulling, then pushing the animal. The forward component of the ground reaction force is aligned with the horizontal meropodite/carpodite pivot, which allows retraction but resists anteroposterior bending. The vertical carpodite/propodite joint appropriately resists posterior bending in the power stroke, but can flex forward a little during recovery, allowing the leg to brush past obstacles on a rough substratum. The last leg pair are smaller and thrust backwards, but weakly. Their movement consists mainly of extension about the meropodite/carpodite pivot.

Their limb cross sections are interesting. Instead of the round or slightly elliptical sections typical of insects, myriapods and spiders, those of the first three leg pairs are narrow ellipses, whose long axes are orientated in the plane of limb retraction. The highest second moment of area of the podomere sections is therefore in the direction of the greatest bending moments, the sections are streamlined relative to the movement of the limb, and the flexor and extensor muscles gain space and mechanical advantage. Logical so far: but the third leg pair is similarly shaped, and the long axis of its section is normal to the direction of thrust, suggesting that the last two functions may be the most significant. The weak last pair have more-or-less cylindrical podomeres.

Carcinus maenas, the shore crab, can move forwards or backwards by the usual combination of promotion/remotion and flexion/extension, but its preferred gait is sideways, with the flexion and extension of the limbs providing the thrust (Manton, 1977). The orientation of the limb joints is similar to that of crayfish, but with one fewer basal podomere and no terminal dactyl. The sections of the podomeres are again thin ellipses whose long axis is aligned with the plane of flexion and, in this case, of movement. The most posterior legs are flattened distally and are held horizontally and usually clear of the substratum. They appear scarcely to contribute to the walking movement. The crabs hardly swim, but the legs may serve to stabilise the animals in, for example, falling from a rock, perhaps generating some lift in the manner of the portunid crabs, whose hind limbs are similarly but more fully developed (Plotnick, 1985; Azuma, 1992).

In these Decapoda, available locomotory patterns are again closely associated with the alignment and directional flexibility of the joints, but the appendages are under full muscular control. The sequentially differential orientation of the joints gives considerable gait flexibility: just as Carcinus can walk forwards if need be, prawns, e.g. Leander, can switch from the preferred forward walk to lateral crabwise movement at will, using the limb retractors for thrust.

Both crayfish and crabs are capable of walking in water and in air, and both provide good opportunities for a comparison of gaits in the two media (Hui, 1992; Martinez et al., 1998).

Drag-based swimming

Errant polychaetes, most Crustacea, adult water-beetles and adult and juvenile aquatic Hemiptera swim using paddles. The range of appendages is huge, but most are flattened or bear numerous stiff bristles, often both. The appendages of some (the legs of hydrophilid beetles and Pycnogonida and the pereiopods of munnopsid isopods) move independently on the two sides of the body, those of hydrophilids and munnopsids in modified walking patterns, those of pycnogonids in sequence from rear to front. The appendages of others operate as a single, simultaneously stroking pair: the metathoracic legs of most water beetles and bugs and the antennae of Cladocera, Ostracoda and Copepoda. The appendages of yet others, such as the parapodia of polychaete epitokes (Clark, 1961), the phyllopods of notostracan, anostracan and leptostracan Crustacea and the pleopods of swimming decapods and most swimming isopods, operate in serial sequence, beating metachronally. The kinematic patterns of many are well-known (Cannon, 1933; Nachtigall, 1980, 1985; Alexander, 1988; Hessler, 1993; Daniel, 1995; Koehl, 1995).
Typically, paddles are adapted to maximise drag in the effector stroke and to reduce it in the recovery stroke by bending, torsion, change of section and/or effective area. Much of this deformation is certainly drag-assisted and made possible by asymmetric flexural and/or torsional compliance in the appendages. In contrast with walking, in which torsion is potentially highly damaging (Gordon, 1978), it can now be advantageous. Most crustacean phyllopods are asymmetric in planform, and the two rami (branches) of malacostracan pleopods are usually unequal, so that some passive torsion is probable. Bending is certainly crucial. Fig. 5 shows a pleopod of *Leander*. The slender, leaf-like endopodite articulates with the basipodite by a broad, nearly vertical hinge and can twist to reduce drag on the recovery stroke. The larger exopodite has a moncondylar joint with the basipodite and can swing sideways to increase or reduce the effective frontal area. During the effector stroke, the pleopod is straight, with the endopodite and exopodite spread. During the recovery, they flex and lie together. As in the swimming appendages of most swimming Crustacea, aquatic Hemiptera and Coleoptera and many insect larvae, the pleopods of *Leander* carry long articulated setae, and these are themselves multibranched, with serial setulae. Like the podomeres that bear them, the hairs are asymmetrically hinged, articulated to the ramus by a single condyle. Each bristle is actively erected for the propulsive stroke by an individual slender muscle, but folds automatically for the recovery stroke, presumably under the influence of drag. In the swimming legs of dytiscid and gyrinid beetles, however, both the erection and folding of the bristles appear to occur automatically under hydrodynamic pressure (Nachtingall, 1980).

A few arthropods are able to swim with long filiform legs. The total leg length of *Nymphon* (Pycnogonida) can be as much as 600 mm on a 12 mm body. It typically treads water with its legs operating in postero-anterior series (Morgan, 1971). In the remarkable deep-sea munnopsid Isopoda, Marshall and Diebel (1995) have identified four distinct gaits. Three involve the pleopods, but the fourth is carried out by the elongate pereiopods, with which the animals ‘walk’ through the water. Their tips carry long, folding hairs. Not only do the latter erect and fold automatically, but the terminal leg segments apparently also lack muscles: a uniquely high degree of automation in an arthropod leg.

**Flying in water and air: mollusc fins and insect wings**

In drag-based swimming, active and/or automatic flexion on the recovery stroke is general and torsion not unusual. In lift-based propulsion, torsion is virtually essential if force asymmetry between half-strokes is to be achieved, and bending, if present, needs to be tightly controlled. In water, lift-based locomotion occurs in portunid crabs, using the last pair of legs (Plotnick, 1985; Azuma, 1992), and in some cephalopod and gastropod molluscs. The insects are the only invertebrate aerial fliers.

**The flying fins of squids and pteropods**

In the Mollusca, paired locomotory appendages are found only among Cephalopoda (Packard, 1972; Hoar et al., 1994) and Gastropoda (Farmer, 1970; Satterlie et al., 1985). Shapes vary from the ultra low-aspect-ratio undulatory fins of *Sepia* (Kier, 1989) to the short, flapping triangles of loliginid and ommastrephid squids and the quadrilaterals of some pteropod gastropods. The fins of cephalopods show a range of complex propulsory movements resembling those of skates and rays (Hoar et al., 1994), and some ommastrephid squids show remarkably flight-like movements, with the fins clearly operating as lift generators. The swimming kinematic patterns of *Clione limacina*, a pteropod prosobranch mollusc, are strikingly similar to those of hovering hawkmoths, apparently even paralleling the ‘clap-and-fling’ method of unsteady lift production of many flying insects (Satterlie et al., 1985). Yet the means by which these effects are achieved represent opposite ends of the automation spectrum. *Clione* fins are hydrostats with no rigid components, and the deformations of these and other mollusc fins are entirely under muscular and neurosensory control. Significant torsion is visible, necessarily distally to the fin base, since the latter is broad in every case. In *Clione*, hydrodynamically generated torsional moments may assist twisting at some stages of the stroke. Their magnitude,
as in all hydrofoils and aerofoils, depends on the relative positions of the centre of torsion and the centre of lift. The anteroposterior symmetry of most squid fins suggests a torsion centre close to the mid-chord, so that moments will probably be small. *Clione* parapodia, however, are rather diamond-shaped and show some anteroposterior asymmetry, so that these moments will be relatively larger.

**Insect wings: automation and fully remote control**

Swimming appendages, whether operating by lift or by drag, tend to be short, sturdy and muscular. Wings need to be large, with minimal inertia, and those of insects have no internal muscles at all. All the cyclic deformation necessary for force asymmetry must therefore be remotely controlled from the base and partly or wholly automatic, encoded in the structure and in the distribution of material properties throughout the wing (Wootton, 1981, 1992).

Torsion is important in determining and altering the wings’ angle of attack. The basal muscles are capable of actively pronating and supinating the whole wing, but high-speed still photographs and cine film show that most insect wings are to some extent twisted like aircraft propellers along their length during translatory movement, reflecting the base-to-tip gradient in relative wind speed and in the direction of incident flow. This spanwise torsion is largely automatic and principally due to aerodynamic and inertial torques (Ennos, 1988a,b) resulting from the general asymmetry of the planform and the distribution of the supporting veins. Many wings are expanded posteriorly and, even when they are relatively elliptical, the principal supporting veins are closer to the leading than to the trailing edge and the longitudinal veins tend to be curved, favouring the chordwise transmission of torsional moments. In combination with spanwise torsion, vein curvature has the additional important effect of automatically depressing the trailing edge and imposing a camber on the wing in direct response to aerodynamic loading (Newman, 1982; Ennos, 1988a; Wootton, 1991, 1992).

Insect wings are enormously varied in shape and structure, reflecting the great diversity of the group and their wide range of flight techniques, performance and behaviour. Their functional morphology and mechanics in flight and in folding have been investigated in detail in many groups, particularly Ephemeroptera (Brodsky, 1971), Odonata (Newman, 1982; Newman and Wootton, 1986; Pfau, 1986), Plecoptera (Brodsky, 1979, 1981, 1982), Hemiptera (Betts, 1986a,b; Betts and Wootton, 1988; Wootton, 1996), Diptera (Ennos, 1988a,b, 1989; Wootton and Ennos, 1989), Mecoptera (Ennos and Wootton, 1989), Orthoptera (Jensen, 1956; Zamack, 1972, 1982; Pfau, 1977; Wootton, 1995), Coleoptera (Brackenbury, 1994; Haas and Wootton, 1996), a range of Lepidoptera (Wasserthal, 1974; Grodnitsky and Kozlov, 1985, 1990; Wootton, 1993), of Holometabola in general (Grodnitsky and Morozov, 1995) and of Palaeozoic Paleoptera (Wootton and Kukalová-Peck, 1999) (for general accounts, see Wootton, 1992; Brodsky, 1994). These have revealed a remarkable array of adaptations, some of which are independent enough of the insect’s musculature to be considered as ‘smart’ structures, automatically adjusting the section and attitude of the wing in direct response to the aerodynamic and inertial loading.

To illustrate how basal muscles, wing morphology and external forces can interact to determine instantaneous wing shape and deformation in flight, we will consider the general question of the control of ventral transverse flexion. The wings of many insects flex ventrally at the end of the downstroke (Nachtigall, 1966; Weis-Fogh, 1973; Dalton, 1975; Wootton, 1981; Ivanov, 1985; Betts, 1986a,b; Ennos and Wootton, 1989; Brackenbury, 1992, 1994; Zanker and Götz, 1990). This may serve several functions, not all of which are yet clearly understood, and it takes several forms (Wootton, 1981). Sometimes, as in many Diptera and in the parasitic wasp *Encarsia formosa* (Weis-Fogh, 1973), the whole wing flexes near the base and straightens quickly during the upstroke (Fig. 6A), almost certainly creating unsteady lift (Zanker and Götz, 1990). Sometimes, as in many Plecoptera, Mecoptera, Hemiptera, Megaloptera, Trichoptera and Lepidoptera, the whole wing-tip bends ventrally and stays flexed for much of the upstroke (Fig. 6B). Sometimes the leading edge stays almost straight, but the rest of the wing flexes along an oblique curved line (Fig. 6C). Both these latter situations serve to create a ventrally convex camber in the distal part of the wing and to modify its angle of attack, allowing favourably directed lift during the upstroke. Ventral flexion permits many insects to gain a greater degree of distal torsion than is allowed by the structure of the wing base, and often, in combination with a nearly horizontal stroke-plane, to gain weight support on the
morphological upstroke as well as the downstroke, so allowing slow flight and hovering. Flexion is presumably initiated by the inertia of the wing and the added mass of air as the wings decelerate at stroke reversal, but can be maintained and augmented during the morphological upstroke by aerodynamic pressure on the morphologically dorsal, though now functionally ventral, side of the wing.

In some cases, flexion takes place over a large part of the wing-span, with a large radius of bending (Fig. 6D), but in many it is localised along a clear line that may be marked by thinning or zones of soft cuticle in the veins or an abrupt change in the overall rigidity of the wing structure (Wootton, 1981). In some Diptera and Hemiptera, flexion may take places at two sites in the wing, and in Miridae at least this can happen either separately or simultaneously (Betts, 1986a,b; Brackenbury, 1992) (see Fig. 10B).

How is this flexion controlled? In a thin structure such as a wing there is limited scope for hinge joints of the kind we have seen in arthropod limbs, with an articulation between adjacent hard elements on one side and a segment of flexible cuticle on the other. Something similar, however, is found in the veins of cicadoid Hemiptera, where the transverse flexion line is particularly clearly defined (Wootton, 1981). Frequently, however, the location of the line appears primarily to be determined by the form of the principal supporting veins, by generally lower rigidity in the area between these veins and, crucially, by the profile of the basal part of the wing.

The wings, or at least the fore wings, of most neopterous (wing-folding) insects consist of a main area, the ‘remigium’, and a posterior area, the ‘clavus’, hinged to the remigium along a long flexion line. The area of the remigium proximal to any transverse flexion line is frequently cambered, and in most groups it is longitudinally divided by another flexion line, the ‘median flexion line’ (Wootton, 1979), which allows the camber to be altered actively by pronating and supinating muscles at the base.

Complete structural modelling of an insect wing, either numerically or physically, is complex and time-consuming, but much can be learned as a first approximation by treating it as a thin plate or shell. A cantilevered flat plate, loaded in bending, is equally flexible either way up (Fig. 7A). A cambered plate, in contrast, is markedly asymmetric in flexural rigidity. A force applied from the convex side, however, tends to flatten the section and lower the second moment of area, and the shell eventually bends, with a small radius of curvature, along a line where the section is totally flat. If this line is straight, the camber of the base will decrease linearly from the base to the line of bending and increase linearly beyond it, remaining dorsally convex throughout (Fig. 7B).

If flexion is encouraged to take place along a preformed curved or angled flexion line, however, the structure is now bistable. When unbent, the curvature is uniformly dorsally convex (Fig. 7C). When bent, the distal region snaps across to a second stable position in which the section is dorsally concave (Fig. 7D), and its height and angle relative to its previous longitudinal axis are precisely determined by geometry: the height of the basal camber and the shape of the flexion line. If the anterior and posterior ends of the flexion line are equidistant from the base of the shell, the alignment of the induced concave camber is parallel to the sides. If the flexion line is oblique, however, the apex of the induced camber approximately bisects the curve, or angle, of the flexion line (Fig. 7E).

If we apply this to a real wing, the implication is that the orientation of the reverse camber induced by inertial and aerodynamic forces at stroke reversal is significantly determined by the shape and orientation of the line of transverse flexion. This is beautifully demonstrated by the scorpionfly Panorpa (Mecoptera) (Fig. 8). The fore and hind wings of this insect (Fig. 8A) are rather similar and are not coupled together in flight, so that they bend and twist independently. The subcostal vein (Sc) of each wing, together with the more anterior costa (C) and the more posterior radius (R), form a high-relief supporting spar at the leading edge, and the anterior and posterior cubitus veins (CuA and CuP) provide a firm posterior support. A flexion line runs across the wing from the end of CuA via a desclerotised area at the fork of the median vein (M) approximately to the end of Sc. In the fore wing, Sc is longer than CuA, and the flexion line is tilted anterodistally. In the hind wing, Sc is shorter than CuA, and the flexion line is if anything tilted anteroproximally. High-speed film of the insects in free flight show the very different positions assumed by the wing pairs during the upstroke (Fig. 8B). The aerodynamic implications are discussed by Ennos and Wootton (1989).

In real wings, bending and twisting will be further influenced by the distribution of structural flexibility. Some of this will be inbuilt, but it may also be actively modifiable by
altering the amount of camber in the basal part of the remigium. If this is low, the second moment of area at the flexion line will be low and the wing will bend more readily. Fig. 9 shows a diagrammatic wing of thickness $t$ arched along a longitudinal flexion line. The second moment of area $I$ about the neutral plane is given by:

$$I = 4H^2t^3/3 \cos \alpha,$$

where $H$ is the distance from the neutral plane to the apex of the section and $\alpha$ is half the angle included at that apex. For small deflections, and ignoring buckling, the flexural rigidity will therefore increase by rather less than the third power of the height of the section, which is under fine control from the muscles of the wing base.

The functioning of the flexion lines is particularly clear in the heteropterous bugs, whose fore wings have a thickened proximal section, the ‘corium’, and an unthickened distal section, the ‘membrane’. The boundary between the two forms a transverse flexion line. Within the corium, there is normally a clearly defined median flexion line that approaches, but stops short of, the corium/membrane boundary. However, since the distal end of the corium is moderately compliant, flexing of the proximal part along the median flexion line can alter the camber along the boundary and control the wing’s resistance to ventral bending.

In several families, of which the Miridae is the most prominent, the corium boundary is oblique, and there is a second, more proximal, flexion line, the ‘cuneal fracture’, perpendicular to the leading edge (Fig. 10A). High-speed cine film of two Stenodema species in free flight indicates that flexion along the corium margin is habitual in the upstroke but that flexion at the cuneal fracture is less common, although it does occur (Fig. 10B). It seems probable that, by adjusting the camber of the wing base, the bug is capable of determining whether, under a given external load, the wing flexes along both the cuneal fracture and the distal flexion line (Fig. 10B) or at the latter alone (Betts, 1986a,b).

**Discussion**

What factors, then, influence the design of invertebrate propulsive appendages?

Muscular hydrostats can function in aquatic substratum locomotion and in drag-based and lift-based swimming, and the Onychophora demonstrate that they can operate well on land, with a surprising range of gaits (Manton, 1950). However, exoskeletal appendages give scope for far greater locomotory versatility in both water and air.

Walking legs in the various arthropod classes have some fundamental similarities, but vary greatly in relative length, in proportions and in the number of podomeres and the sequence and orientation of joints. Not all these differences are easily interpreted. Long legs can be adapted (a) for fast walking or running, (b) for stepping over gaps in vegetation, (c) for raising the body above a dangerously hot substratum, (d) for special types of prey-capture, (e) for locomotion on the surface film of water bodies, and also for various combinations of these. Scutigeromorph centipedes, many lycosid spiders and the ant *Cataglyphis* probably combine a and c; many Opilionida and
The spider *Pisaura* combine a and b; the spider *Dolomedes* combines a and e. Most stick-insects (Phasmda) fit b; hydrometrid and gerrid Hemiptera fit e; thomisid and pholcid spiders fit d.

Podomere number is hard to interpret, except in general terms. More joints can lead to faster locomotion because of summation of angular velocities down the leg, but it need not. Most arthropod legs have degrees of freedom to spare, but extra joints can achieve similar movements with smaller flexion angles at each, minimising soft cuticle and probably gaining in strength, may increase the number of possible foot positions within the total field of movement of the limb, and may also help to minimise the bending moments about individual joints. As we have seen, the distribution of pivot and hinge joints is to some extent logical, but it remains obscure why myriapods and arachnids have only hinge joints and therefore only flexor muscles in the distal parts of their legs. It may allow more slender legs, but the sturdy legs of millipedes are constructed similarly, and the legs of many Pycnogonida and Diptera are equally filamentous.

Of the various locomotory options, drag-based swimming appears to make fewest demands on appendage design. Given near-neutral buoyancy, all that is required is a muscular paddle that is erected for the power stroke but folds, twists or retracts for the recovery. A flat paddle would serve, but a curved section, concave in the direction of the power stroke, is stiffer and gives higher drag coefficients. Hydrostatic paddles, as usual, need total muscular control, but an arthropod exoskeletal one could function with one powerful extrinsic muscle inserted near the base. This would be necessary to drive the power stroke but, provided that any joints were correctly orientated and constructed to deform only on the recovery stroke, other deformations could in theory be driven by drag alone.

These are minimum requirements. In practice, arthropod swimming paddles are usually far more complex, with a suite of adaptations, skeletal and muscular, for maximising and directing thrust and minimising drag on recovery. These are particularly evident when few appendages are involved, as with the swimming legs of aquatic Coleoptera and Heteroptera. Crustacean phyllopodia are broad and lobed. The pleopods and uropods of Malacostraca are normally biramous, and the rami are capable of being spread for the power stroke and overlapped for the recovery. Hinged fringing hairs, often branched, spread to enhance the drag and fold automatically to minimise it. The situation is complicated by the fact that many swimming appendages are also concerned in creating feeding currents, or filtering, or both. Nonetheless, drag is extensively recruited to assist deformation, and the latter is controlled at least partly by the skeletal architecture and properties.

If drag-based swimming is the mode of locomotion least demanding on appendage design, flight must be the most. Insect flight is costly, and flight muscle is surprisingly inefficient. It is increasingly clear that most insects could not support their weight in air without resorting to unsteady aerodynamic mechanisms and without gaining useful force on both the downstroke and upstroke: ‘feathering’ for a recovery stroke is seldom adequate. These measures require torsion, often with transverse bending, and any of a range of other deformations including camber alteration, fanwise bending along a series of flexible lines radiating from the wing-base and alteration of effective area. They must happen without sacrificing essential rigidity and without allowing the wing to swing up into the wind like a flag. They must take place at frequencies that may reach several hundred hertz and be capable of rapid alteration as the insect accelerates, manoeuvres and compensates for changes in ambient flow.

All this must be achieved without internal musculature. The wings are ultra light, with minimal mass, but even so inertial forces are often well in excess of aerodynamic forces. Basal attitude and camber are determined by the relative movement of nearby thoracic sclerites and by muscles pulling directly on the wing anteriorly and posteriorly to the pleural fulcrum over which it is flapped, but their influence on wing shape is remote and limited. Shape is otherwise determined by the overall elastic response, encoded in the wing’s structure and materials, to the instantaneous patterns of aerodynamic pressures and inertial stress throughout the stroke. Insect wings hence represent a high spot in skeletal engineering and the culmination of automation in appendage functioning. Their status as ‘smart’ aerofoils, structures responding autonomously and advantageously to external forces, is perhaps unparalleled in the animal kingdom.
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Invertebrate paraxial locomotory appendages 3343


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