

# Hypaxial Motor Patterns and the Function of Epipubic Bones in Primitive Mammals

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Since the first description of epipubic bones in 1698, their functions and those of the associated abdominal muscles of monotremes and marsupial mammals have remained unresolved. We show that each epipubic bone is part of a kinetic linkage extending from the femur, by way of the pectineus muscle, to the epipubic bone, through the pyramidalis and rectus abdominis muscles on one side of the abdomen, and through the contralateral external and internal oblique muscles to the vertebrae and ribs of the opposite side. This muscle series is activated synchronously as the femur and contralateral forelimb are retracted during the stance phase in locomotion. The epipubic bone acts as a lever that is retracted (depressed) to stiffen the trunk between the diagonal limbs that support the body during each step. This cross-couplet kinetic linkage and the stiffening function of the epipubic bone appear to be the primitive conditions for mammals.

Except for the extant placental mammals (crown-group Eutheria), all mammalian taxa and their immediate cynodont ancestors possess epipubic bones—a pair of bones articulating with the pelvis that project anterolaterally into the hypaxial muscle layers of the abdomen (1). Epipubic bones articulate from the pubic rami with a hingelike synovial joint, and when depressed each bone swings ventrolaterally in the belly wall. They are homologous to the nonarticulating anterior pubic processes of the primitive pubeoschiatic plate of amniotes (2). Epipubic bones first appear in the Tritylodontidae (a cynodont outgroup to the Mammalia) and are retained as a primitive character in all extinct nontherian mammals (for which postcranial material is available) and all living monotremes and marsupials (1, 3). Within the Eutheria, they are present in the stem eutherians but have been lost in all extant placental mammals (1, 4).

All mammals have four abdominal hypaxial muscle layers (Fig. 1): two obliquely crossing layers (internal and external obliques), one longitudinal layer (rectus abdominis) and one transverse layer (transversus abdominis, not shown in Fig. 1). Mammals with epipubic bones have an additional hypaxial muscle, the pyramidalis, that extends anteriorly from the medial aspect of the epipubic bones to the linea alba (Fig. 1). Because all of these muscles (which are paired) would act to elevate the belly and the epipubic bones, bilateral activity in all of these

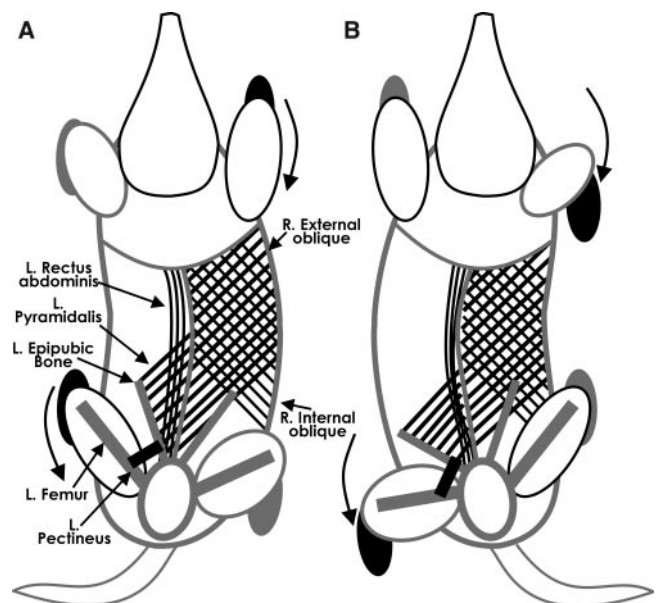
muscles has been proposed as a mechanism to support the pouch or young attached to the belly (3, 5). The generality of this function is questionable, however, as it implicitly assumes that epipubic bones are only functional in females bearing young; it does not address function in males. The likelihood is extremely small that females of extinct taxa, such as advanced cynodonts, stem eutherians, or all primitive mammals, possessed a marsupium or bore altricial young attached to mammary glands. Furthermore, epipubic bones are usually connected to the femur by an appendicular muscle, the pectineus muscle, that originates on the proximal lateral aspect of the

epipubic bone and inserts along the midshaft of the femur. Because of this connection to the femur, it has been proposed that in the generalized mammalian condition the epipubic bones act unilaterally with unilateral activity in the pectineus to assist in protracting the femur during swing phase of symmetrical gaits (for example, walks and trots) (3).

We studied motor patterns in the abdominal hypaxial muscles of the gray short-tailed opossum (*Monodelphis domestica*) and the Virginia opossum (*Didelphis virginiana*) during treadmill locomotion (6). The animals used only symmetrical gaits (i.e., each step is dominated by diagonal couplets of support). As in generalized amniotes, these species do not exhibit asymmetrical gaits (such as bounds) during sustained locomotion (7). Electromyograms (EMGs) were recorded bilaterally from each muscle, and footfall patterns were obtained from simultaneous high-speed video recordings of each step. Both species exhibited an asymmetrical pattern of muscle activation, in which the pectineus, pyramidalis, and rectus abdominis on one side fired in concert with the internal and external oblique muscles of the opposite side (Fig. 2) over the full range of velocities studied. Thus, during the stance phase of each diagonal limb pair, there is a direct line of muscular tension between the retracting femur and the opposite body wall that stiffens the body across the limb couplet. Simultaneously, the trunk is bent laterally, presumably by the epaxial muscles with a possible contribution from the oblique abdominal muscles (6).

Videofluoroscopy (8) revealed that in both species, each epipubic bone is depressed when

**Fig. 1.** Cross-couplet hypaxial muscle function in primitive mammals. As the left hindlimb–right forelimb couplet (black shaded feet) retracts from foot down (A) to foot up (B), hypaxial muscles (black bars) fire in an asymmetrical pattern reaching from the stance hindlimb to the rib cage on the opposite side. Left femoral retraction and tetanus in the left pectineus muscle retracts (depresses) the left epipubic bone, which increases tension on the muscle series extending through the left pyramidalis and rectus abdominis, linea alba (midline in gray), to the right internal and external oblique muscles. This kinetic linkage stiffens the body across the limb pair and bends the body to the right, presumably in concert with the epaxial musculature. The pyramidalis muscle and epipubic attachment of the pectineus muscle are unique to mammals with epipubic bones.



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the ipsilateral hindlimb retracts and elevated when it protracts. Thus, as the femur retracts, the pectineus contracts to depress the epipubic bone on its hinge joint, which pulls on the line of contracting muscles extending diagonally across the belly to the opposite side of the trunk. Electromyograms suggest that the pectineus is actively resisting lengthening and, thus, acts as a ligament; therefore, other muscles retracting the limb may contribute to the depression of the epipubic bone and stiffening of the body. These data indicate that the epipubic bone is acting as a lever to facilitate stiffening of the body across the limb pair that is on the ground. Elevation of each epipubic bone occurs rapidly late in the stance phase when femoral protraction begins, because the pectineus goes silent before the pyramidalis and obliques and the latter muscles elevate the epipubic bone. Because the epipubic bone is fully elevated throughout the swing phase and the pectineus is silent, these bones cannot be functioning in femoral protraction.

The functions of the hypaxial abdominal muscles during locomotion in tetrapods have rarely been investigated and thus remain poorly understood. They have been proposed to aid in lateral bending in salamanders and lizards (9–11), to resist long-axis rotational forces in salamanders and lizards (9, 10, 12), and to resist sagittal bending in dogs (13). Our results show that in mammals with epipubic bones, epipubic movements during femoral retraction and cross-

couplet muscle activation transmit muscular stresses obliquely through the abdomen from the hindlimb to the contralateral body wall and forelimb. Muscle activation patterns presented here suggest that three of these muscles retain much of the functions observed in other tetrapods. Specifically, the external and internal obliques aid in lateral bending (though this role is reduced in mammals relative to generalized tetrapods) and the rectus abdominis stiffens the trunk longitudinally to prevent sagittal bending. We observed the following motor patterns: (i) activity of the rectus abdominis contralateral to lateral bending; (ii) activity of the pyramidalis muscle, linking the epipubic bone to the contralateral oblique muscles; (iii) activity in the pectineus, linking the mobile epipubic bone to the pelvic limb; and (iv) the integrated activation of these muscles with the retained primitive functions of the contralateral oblique muscles. We hypothesize that all four of these motor patterns work in concert to resist long-axis torsional bending that results from ground reaction forces associated with locomotion with diagonal couplets.

We propose that the addition of links from the obliques to the contralateral pyramidalis, to the jointed epipubic bone, to the pectineus, to the femur, which act together to resist long-axis torsional moments during the step, is unique to the Mammaliaformes and its immediate out-

group the Tritylodontidae. The appearance of this system (based on the appearance of epipubic bones) and its subsequent retention in most mammalian taxa implies a critical innovation in the transition from generalized amniote to mammalian patterns of locomotion. These innovations appear concomitantly with the key mammalian traits of endothermy, mastication, and lactation that require increased locomotor activity and efficiency. Evidence of such a change in locomotory performance is seen not only in the advent of the cross-couplet linkage proposed here, but in the appearance of the mammalian-grade pelvis (reduced pubis and anteriorly projecting ileum) (14) and the change to less sprawling, more parasagittal pelvic limb posture at the level of the tritylodontids (15). Reliance on the cross-couplet system would appear to constrain animals to couplet-dominated symmetrical gaits, which is true for generalized marsupials (for example, *Monodelphis* and *Didelphis*) and monotremes (7). Evidence of release from this gait constraint comes from mammals that have reduced epipubic bones (for example, the extinct Tasmanian tiger) (16) or conjoined epipubic bones (for example, bandicoots), or that have lost the connection of the pectineus with the epipubic bones (such as wombats and large kangaroos and wallabies). These animals use more complex asymmetrical gaits (half bounds, bounds, and gallops) (17, 18), have more erect limb postures, or have shifted to bipedal locomotion.

Though these findings cannot falsify the long-standing hypothesis that epipubic bones support the marsupium (5) or mass of attached young (3), they do demonstrate that the pectineus is inactive during the swing phase and thus cannot participate in femoral protraction. Further, the pectineus is active during the stance phase (femoral retraction), which depresses the epipubic bone, enhancing the action of the pyramidalis and rectus abdominis on one side, and the external and internal obliques on the other. This cross-couplet kinetic linkage serves to resist torsional and sagittal stresses on the trunk that are produced by the appendicular muscles and diagonally supporting limb couplets during locomotion with symmetrical gaits. It is hypothesized that this stiffening function was an important innovation during the reptile-mammal transition that allowed greater locomotor efficiency with erect postures by rendering the axis of the body less compliant to ground reaction and gravitational forces.

References and Notes

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6. Variation in mechanical and activation properties of muscle fibers, tendons, and muscle architecture can

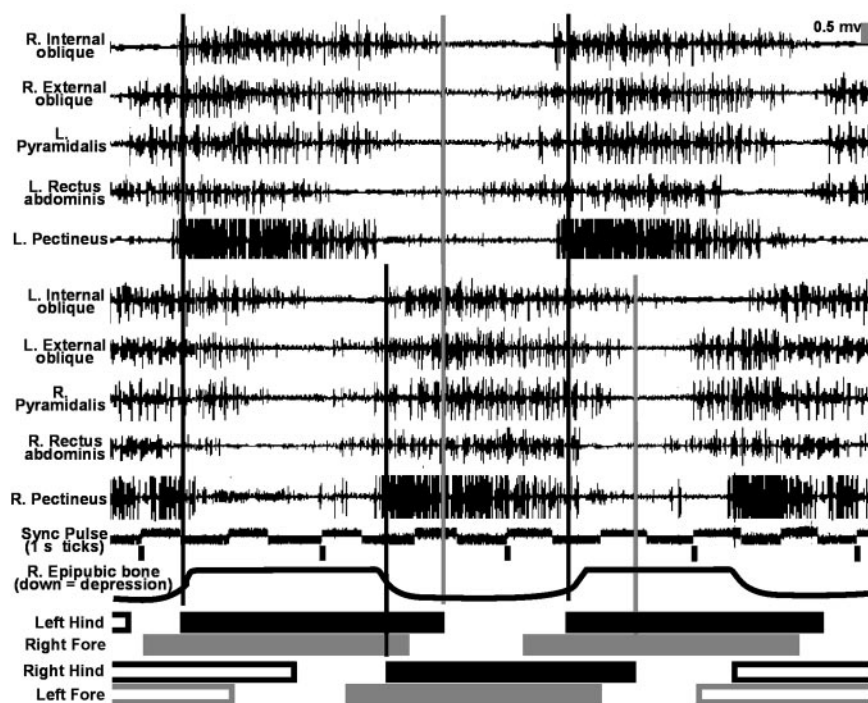


Fig. 2. Asymmetrical hypaxial motor patterns for the Virginia opossum during treadmill locomotion. Electromyograms for the muscles in each cross-couplet linkage are shown relative to the hindlimb stance phases (black bars) for three consecutive couplet stance phases (alternating sets of black and shaded bars). Movements of the epipubic bones (illustrated for the right side visualized from videofluoroscopy) show that each bone is retracted only with the ipsilateral hindlimb. This basic pattern was observed in all strides observed in both opossum species studied. Note the intense bursting patterns in the pectineus muscles.

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affect the interpretation of muscle function from EMGs. Muscle activation may result in isometric or isotonic (even lengthening isotonic) contractions that are impossible to distinguish. However, our interpretations of the contributions of abdominal muscles to trunk bending and of the pectineus muscle to pelvic limb movement are conservative because we account for every muscle that attaches to the epipubic bones. The movements of the epipubic bones can only be produced by the muscles tested. In addition, the muscle activation resulted in musculoskeletal movement, which confirms that tension was generated during the stance phase. Thus, it is irrefutable that the abdominal muscles elevate, and the pectineus depresses these bones.

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was female) were used in the study. Motor patterns were recorded using standard fine-wire electromyography and synchronized high-speed video (at 200 fps) while the animals moved at speeds of 0.15 to 0.50 m s<sup>-1</sup> on a motorized treadmill (19). Limb and epipubic bone movements were videotaped (at 60 fps) using a Picker Corporation Model K2601 videofluoroscope as the animals ran on the same treadmill and speed range. Thin metal rods were implanted along each epipubic bone to visualize epipubic bone movements relative to the pelvis and hindlimb. Animal care and research protocols were in accordance with approved Ohio University Institutional Animal Care and Use Committee guidelines.

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# Wing-Assisted Incline Running and the Evolution of Flight

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Flapping wings of galliform birds are routinely used to produce aerodynamic forces oriented toward the substrate to enhance hindlimb traction. Here, I document this behavior in natural and laboratory settings. Adult birds fully capable of aerial flight preferentially employ wing-assisted incline running (WAIR), rather than flying, to reach elevated refuges (such as cliffs, trees, and boulders). From the day of hatching and before attaining sustained aerial flight, developing ground birds use WAIR to enhance their locomotor performance through improved foot traction, ultimately permitting vertical running. WAIR provides insight from behaviors observable in living birds into the possible role of incipient wings in feathered theropod dinosaurs and offers a previously unstudied explanation for the evolution of avian flight.

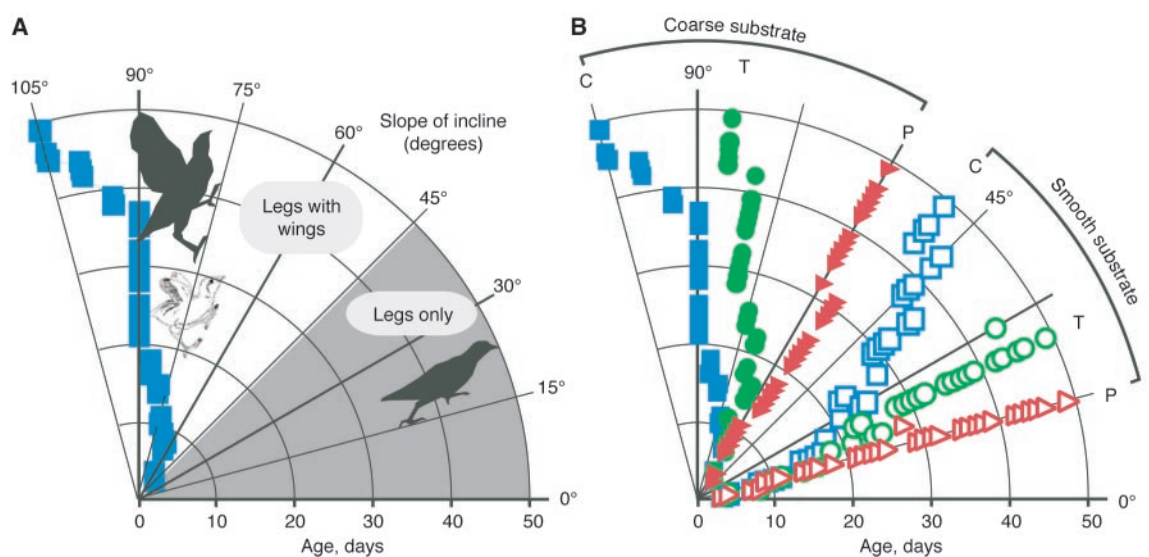
Most species of living birds are altricial, producing naked, thermally dependent, and non-mobile hatchlings that are sequestered in above-ground nests and require substantial

parental investment before independence (1). In contrast, offspring of precocial species (e.g., Galliformes and Tinamiformes) hatch fully feathered and are capable of leaving

their simple ground nests almost immediately to forage and escape predation. From hatching, chukar partridges (*Alectoris chukar*) use their well-developed legs to ascend textured surfaces with inclines of up to 45°. However, chicks can also walk and run up steeper slopes while vigorously beating their developing wings (Fig. 1A). With this strategy, called wing-assisted incline running (WAIR), hatchlings negotiate 50° inclines, 4-day-olds climb 60° slopes, and 20-day-olds accomplish vertical ascents. Mature birds also combine wing and leg movements to scale overhanging slopes of up to 105°, as well as to traverse lower inclines when exhausted from aerial flights. When employing WAIR, birds reach heights of >5 m on vertical surfaces and do not require a running start. Although this behavior is common in nature, WAIR has

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**Fig. 1.** (A) Incline-running performance on a textured substrate (36-grit sandpaper) for chukar partridges with fully feathered (control group) wings during development from posthatching to 50 days. Shaded area represents angles of shallow incline where birds did not recruit their flapping wings. To ascend steep inclines, developing chicks and adults employ WAIR (nonshaded area). (B) Incline-running performance on textured and nontextured (smooth) substrate for chukar partridges possessing fully feathered (control, C), trimmed (T), and plucked (P) wings starting the day after hatching. Data points represent the climbing angle (in 5° increments) that all five individuals within each of the three groups were able to perform that day. Control animals (feathered wings) were capable of vertical running within 20 days of hatching, whereas plucked birds did



not improve incline running performance beyond what they could attain during their first few days posthatching. Birds with trimmed wings and incapable of aerial flight attained intermediate locomotor performance. These data show that hindlimb traction is associated with WAIR performance.