

Description of Surface Swimming by *Hypera eximia* LeConte (Coleoptera: Curculionidae): Behavioral, Morphological, and Phylogenetic Implications

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ABSTRACT Three species of *Hypera* (*H. eximia* LeConte, *H. postica* Gyllenhal, and *H. nigrirostris* F.) exhibit variable leg morphologies and swimming behaviors. We present morphometric and time lapse video data to document the function of each leg in the swimming behaviors of these weevils. Comparisons were made between *H. eximia* and two congeneric species that do not have the capacity to swim. Morphometric analyses and extirpation experiments aided in understanding the roles of each individual pair of legs and how each leg segment contributes to the entire leg's functionality. *Hypera eximia* exhibited a well-developed swimming ability, whereas *H. postica* and *H. nigrirostris* were unable to perform any coordinated swimming activity. The capacity for swimming is associated with the different leg morphology of *H. eximia*. Morphological differences among the three species are significantly different in prothoracic femoral length, tibial length, tarsal width; mesothoracic femoral length and width, tibial length, tarsal width; and metathoracic femoral width. The *H. eximia* swimming behavior is conducted with all three pairs of legs and the rostrum and is manifested in a breast stroke-like maneuver. The prothoracic legs are used primarily in directional movements and buoyancy compensation, whereas the meso- and metathoracic legs are used asynchronously in forward thrust. Propulsion is accomplished via a 2-phase power stroke with thrust of the mesothoracic leg following the metathoracic leg thrust. Swimming appears to have evolved in three distinct curculionid sub-families including the Errrhinae, Ceutorhynchinae, and Hyperinae. We suggest swimming has multiple origins in the Curculionidae and is associated with both behavioral and morphological adaptations.

KEY WORDS *Hypera eximia*, locomotion, Curculionidae, swimming behavior

INSECT LOCOMOTION CAN be categorized into three broad behaviors including walking (or running), flying, and swimming. Each type is characterized by its own distinct mechanical and behavioral properties. Swimming-stroke patterns differ from the walking gait in the pattern of coordinated leg movements. The majority of free-swimming insects occur in larval and pupal stages of Diptera, larval and adult Hemiptera, and larval and adult Coleoptera (Chapman 1998). Nachtigall (1964, 1974 1980, 1985) reviewed swimming behavior in aquatic insects, including many species of aquatic beetles, however, he did not mention weevil swimming of any kind.

To date, most research on aquatic beetle swimming has focused on the behaviors of Dytiscidae (Hughes 1958; Nachtigall 1960, 1961; Gewecke 1980, 1985; Ribera et al. 1997) and Hydrophilidae (Barr and Smith 1980, Pirisinu et al. 1993). Other beetles are known to propel themselves through the water column by

means other than swimming. *Stenus* spp. (Staphylinidae: Coleoptera) are able to expel pygidial gland chemicals (i.e., stenusin) which causes the beetle to attain speeds of 70 cm/s due to hydrophobic reactions between stenusin and the surrounding water (Schildknecht 1972). In addition, swimming has been described for many terrestrial insects (Miller 1972, Franklin et al. 1977, Pflüger and Burrows 1978, DeBois and Jander 1985, and Lockwood et al. 1989).

Research on weevil swimming began with the work by Angus (1966) on *Bagous limosus* (Gyllenhal), which was reported to dive below the water's surface and spend ample time within the water column. This descriptive work illustrated the swimming capabilities of the species and, in particular, noted the use of the meso- and metathoracic legs in propulsion. Surface and sub-surface swimming has been described for other weevil species (Meiner 1970; Morris 1976, 1995; O'Brien and Marshall 1979; Buckingham and Bennett 1981). However, not all weevils are surface and sub-surface swimmers. Hix et al. (2000) described the swimming behavior of *Lissorhoptrus oryzophilus* Kuschel, which dives beneath the water surface to depths

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of 18 cm, a similar note of diving behavior also was made for *B. limosus* (Angus 1966). *Lissorhoptrus oryzophilus* also has a peculiar mode of swimming, which differs from the traditional behavior of the surface swimming taxa. This species propels itself primarily with the mesothoracic legs in contrast to the metathoracic propulsion seen in *Hypera eximia* LeConte and others.

Adaptations for life in aquatic environments are manifested first in locomotory and respiratory systems (Crowson 1981). These adaptations currently are known for the following curculionid genera *Lissorhoptrus*, *Bagous*, *Phytobius*, *Eurychiopsis*, *Hypera*, *Conotrachelus*, and *Sitophilus*. These genera are contained in five distinct tribes within five separate subfamilies and three weevil families. The physical environment of aquatic habitats imposes similar mechanical forces on swimming beetles, whether they employ surface or submerged swimming techniques. Forces such as friction, viscosity, and gravity all act to reduce the forward motion of an organism through water.

The two types of swimming, surface and submerged, are different with regard to the proportion of induced drag imposed on the swimming beetle. Surface swimmers are able to perform the recovery stroke of the swimming cycle in air, a low-density medium (Vogel 1998). This seems to be a substantial advantage to surface-swimming species. However, submerged swimmers are not affected by surface waves that can greatly affect the efficiency of forward propulsion. Therefore, surface and submerged swimmers have evolved different mechanisms for moving through aquatic environments.

Puttler et al. (1973) reported the swimming activity of two Nearctic, noneconomic *Hypera* species, *H. compta* (Say) and *H. paludicola* Warner, as a breast-stroke type motion. Although *H. eximia* was mentioned in this work, no observations were performed on specific details of the swimming activities of this species. A short note by Read, gave a brief description of swimming in *Hypera rumicis* (L.), which was defined as a "definite breast-stroke action" (Read 1982). *Hypera eximia* typically occurs in a semiaquatic environment dominated by its host plant pale dock, *Rumex altissimus* Wood. Most members of the genus are Palearctic and many are pests of crops (Zaslavskiy 1961). Here we had two primary objectives: (1) to describe the swimming behavior and postures of *Hypera eximia*, and (2) to determine what morphological adaptations are inherent with this locomotory action.

Materials and Methods

Parental generations (P) of *H. eximia* and *H. postica* were field-collected from pale dock or alfalfa plants, respectively, in Boone County Missouri during April and May 1999. Before testing, the P generations were allowed to mate and lay eggs. These eggs were reared on their host plants, producing a second (F₁) generation of each species. No live adults of *H. nigrirostris* could be found in the field; therefore there is no P

generation for that species. However, larvae were collected from red clover and reared to produce an F₁ generation of adults. F₁ individuals are hereby defined as naive individuals with no "wild" experience. Both P (when available) and F₁ individuals were used in morphometric and behavioral analyses. All insects were kept at 20–21°C and a photoperiod of 16:8 (L:D) h. Each individual was video taped while swimming and was allowed to recover before extirpation experiments were performed. All morphometric analysis was completed following video observations. Only females were used in the video and morphometric analyses.

Video Observations. In total, 25 weevil specimens from *H. eximia* (8 P, 7 F₁), *H. postica* (4 P, 4 F₁), and *H. nigrirostris* (2 F₁) were recorded with a Javelin Chromochip II (model number JE3462HR) high-resolution color video camera (Javelin Systems, Torrance, CA) attached to a Wild M-5 Apo stereomicroscope (Wild Instruments, Gais, Switzerland). The camera/microscope apparatus was connected to a Panasonic AG-6740 time-lapse videocassette recorder (VCR) connected to a Panasonic Series 1381 color video monitor (Will Electronics, St. Louis, MO). Individual insects were recorded on a 6-h setting to maximize the number of frames per second the VCR would record. All specimens were observed from a dorsal aspect in a 32 cm by 27-cm plastic tub filled with ≈5 cm of tap water. Each individual was recorded from the time of its placement in the center of the tub until it reached the tub wall or sank to the bottom and made no further movements. Those individuals unable to swim were given a maximum submergence time of 30 s. This time was sufficient to initiate any swimming behavior, as demonstrated by *H. eximia*. It began to swim a few seconds after placement into the water. Analysis of all behaviors was conducted on a frame-by-frame basis to monitor all phases of gait during both power and recovery strokes. Most video recordings made were at 12× magnification.

Extirpation Experiments. These experiments were performed on *H. eximia* to determine the function of each pair of legs during the recovery and power strokes. The extirpations included removal of prothoracic legs, mesothoracic legs, metathoracic legs, and combinations of legs from each thoracic region. Insects were observed and assessed according to several criteria including the following: ability to stay afloat, ability to maintain forward motion, ability to perform directional movements, and ability to reach the tub wall within 2 min. The first three criteria aid in discerning the function of each set of legs, as well as the function of leg combinations. The latter criterion is based on previous observations, which suggest that *H. eximia* is able to reach the tub wall in less than 1 min. All legs from extirpation trials were discarded and not used in the morphometric analysis.

Measurements. After each video session, pro-, meso-, and metathoracic legs were removed at the proximal end of the femur from five individuals each of *H. eximia* (P and F₁ generations), *H. postica* (P and F₁ generations), and *H. nigrirostris* (F₁ generation). Each set of legs was preserved in ethyl alcohol until

examination. All legs were individually slide-mounted with Permout mounting medium and examined using a Leitz Laborlux S compound microscope (Ernst Leitz, Midland, ON, Canada) at a magnification of $4\times$ ($10\times$ ocular magnification). Measurements were taken using a calibrated ocular micrometer for the following morphological characters: (1) femoral length, (2) femoral width, (3) tibial length, (4) tibial width, (5) tarsal length, (6) tarsal width, (7) length of tarsal claws, and (8) width of tarsal claws.

Femoral length was measured from the basicosta of the femur to the anterior femoro-tibial articulation. The femoral width was measured across its widest point. In all *Hypera* species examined, this position is represented as a distal swelling located approximately one-half to three-quarters of the distance between the basicosta and the femoro-tibial articulation. Tibial length was measured from the femoro-tibial articulation (visible when viewed microscopically) to the tibio-tarsal suture. Tibiae in these species tended to be uniform in width across their entire length, thus width measurements were taken at a point approximately one-half of the distance between the femoro-tibial articulation and the tibio-tarsal suture. Tarsal length was measured from the tibio-tarsal suture to the tip of the terminal tarsomere or pretarsus (tarsal claw). Width measurements were taken at the distal end of the second tarsomere. Tarsal claw measurements were also taken. The length of the tarsal claw was measured from the first externally visible portion of the fourth tarsomere to the tip of the pretarsus. The width of the tarsal claws was measured at the base of the pretarsus at the external location of the unguitactor plate.

Statistical Analysis. Data from the leg measurements were analyzed using the SAS statistical package (SAS Institute 1985). Analysis of variance was performed for all leg character data, and Fisher least significant difference tests were performed to establish significant differences between species and among generations within each species for all parameters.

Results

Swimming, here used to describe coordinated leg movements that enable an individual to propel itself on top of or through the water column, was observed only in *H. eximia*. Both *H. nigrirostris* and *H. postica* were unable to perform any activity resembling swimming behavior, and promptly sank to the tub bottom. These submerged individuals continued to exhibit walking behavior, but were unable to reach the tub sides within 30 s, and were thus retrieved from the tub. *Hypera eximia* remained afloat and after a few seconds began to display a surface swimming behavior. Swimming continued until the beetle reached the side of the tub, after which the beetle climbed up the side. All 15 specimens were able to reach the tub wall within 60 s.

Each of the 15 *H. eximia* specimens exhibited the same swimming style. This swimming style is best described as a three-stage behavior including a resting/start stage, power-stroke stage, and recovery-

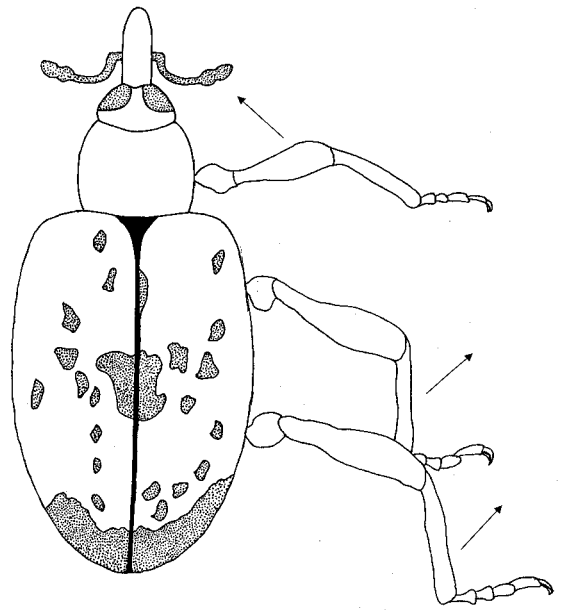


Fig. 1. Intermittent or resting stage, during *H. eximia* swimming behaviors. Note the outstretched appendages to increase the surface area of the weevil in contact with the water. Legs are shown disarticulated from the body to illustrate the position of the coxae.

stroke stage. The resting/start stage was exhibited before initiation of the recovery and power stroke stages. This intermittent stage is denoted by the meso- and metathoracic legs laterally outstretched from the body, at 0° from a transverse plane dissecting each of the coxal cavities (Fig. 1). The prothoracic legs are bent at the femoro-tibial articulation ($\approx 45^\circ$ forward) and the tibio-tarsal articulation ($\approx 45^\circ$ backward). The meso- and metatarsal claws are both angled forward at $\approx 35\text{--}40^\circ$ and the protarsal claws are held perpendicular to the body. The rostrum, or snout, of the weevil is held slightly above the water surface during this stage. The outstretched limbs confer the greatest amount of body contact with the water surface. This increased surface area in contact with the water adds stability to the weevil in the resting position.

Time lapse video observations demonstrated that the power-stroke stage consists of two actions: (1) a primary thrust performed by the metathoracic legs (Fig. 2), and (2) a secondary thrust by the mesothoracic legs (Fig. 3). The first thrust provides the greatest forward propulsion and is characterized by the posterior movement of the metathoracic legs from a perpendicular to parallel position behind the elytral apex. This primary phase is also the shortest phase of the power stroke, lasting less than two frames or ≈ 0.125 s. The secondary phase also provides forward thrust, though not proportional with the primary phase. The secondary phase is characterized by the posterior movement of the mesothoracic legs, until they reach a nearly parallel position adjacent to the metathoracic legs. During the diphasic power stroke, the protho-

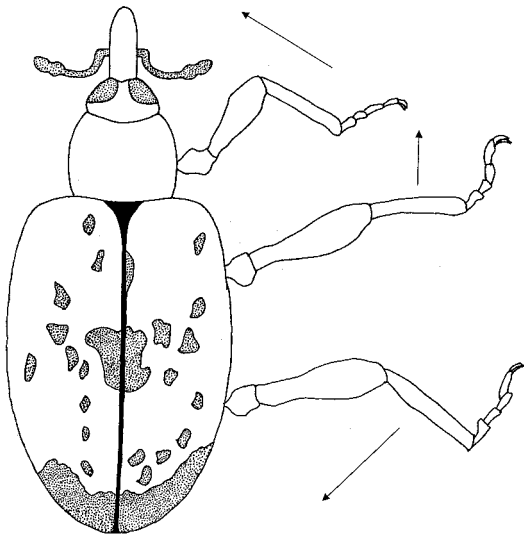


Fig. 2. Primary thrust phase of the power stroke. Arrows indicate the direction the legs are moving as the phase progresses. Legs are shown disarticulated from the body to illustrate the position of the coxae.

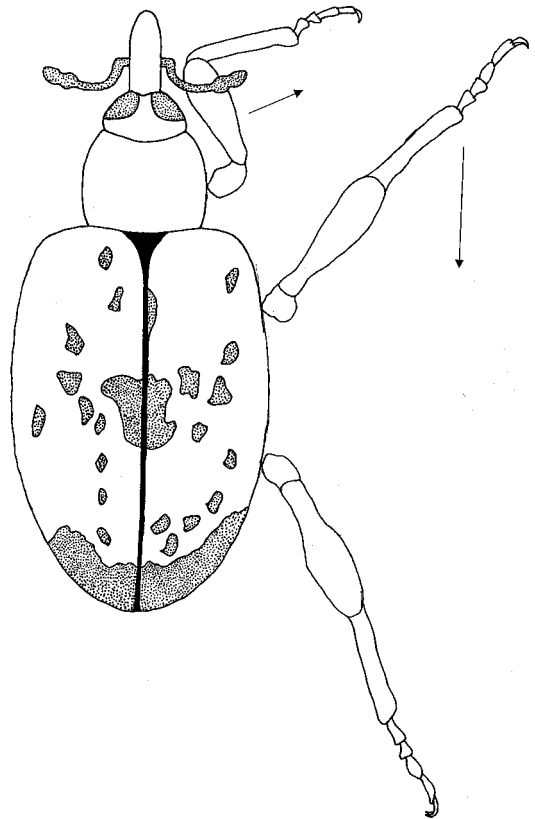


Fig. 3. Secondary thrust phase of the power stroke. Arrows indicate the direction the legs are moving as the phase progresses. Legs are shown disarticulated from the body to illustrate the position of the coxae.

racic legs are rotated anterior into a "mantis-like" position with the femur rotated forward from a transverse plane to 10° , the tibia rotated medially, and the tarsi and tarsal claws rotated laterally. Finally, the rostrum is dipped into the water column at the initiation of the power stroke and remains submerged throughout the duration of the power-stroke.

The recovery-stroke stage, like the power stroke, is also delimited by two distinct phases: (1) extension and retraction of the prothoracic legs (Fig. 4), and (2) retraction of the meso- and metathoracic legs (Fig. 5). As the weevil begins to decelerate, the prothoracic legs are completely extended forward, such that all legs are at their fullest extension and closest to the body midline. After this final extension, the prothoracic legs are retracted to the resting stage in a gradual motion, taking almost 0.25 s to complete. Once the prothoracic legs have come to rest, the meso- and metathoracic legs are also returned to their resting-stage. This part of the recovery stroke occurs more rapidly, taking less than half the time of the prothoracic retraction. During recovery, the rostrum is retracted away from the water surface.

The total time spent in all stages of swimming, i.e., the stroke cycle, is <1 s. The power-stroke, on average, lasted for <0.3 s, and the recovery-stroke ≈ 0.4 – 0.5 s. The resting phase was quite short, typically lasting only one frame or 0.0625 s. This time is much less than that of other swimming weevils (e.g., *Lissorhoptrus oryzophilus*) (Hix et al. 2000). Before contact with the tub side, the weevils exhibited the resting phase of the swimming stages, and glided to the side. These gliding periods were not used for calculating the amount of time spent in each of the stages due to its conclusion in nonswimming locomotion. Swimming speeds in weevils are rather slow, typically in the range of 2–3

cm/s (Crowson 1981). We calculated swimming speeds in *H. eximia* to fall within this range at 2.2 cm/s.

Morphometric Analysis. Morphometric analysis is useful in identifying morphological variation that may contribute to differences in swimming efficacy (Marcus 1990). Mean lengths and widths for all leg segments analyzed are presented in Table 1. Intraspecific variation (i.e., variation between generations) can be explained as differences in size of the individuals studied. Individuals were not discounted based on overall size of the adult. Thus, these whole-body size differences can account for some of the variance between generations.

Videotape analysis of the swimming of *H. eximia* intact and with one or more pairs of legs removed demonstrated a unique pattern of motion that could best be explained by assigning specific functions to each set of legs. Prothoracic legs appeared to be important for orientation and direction of motion. Mesothoracic legs were used primarily to stabilize the weevil while swimming by providing surface tension that allowed the insect to remain upright. The metathoracic legs were responsible for providing the locomotion for the weevil.

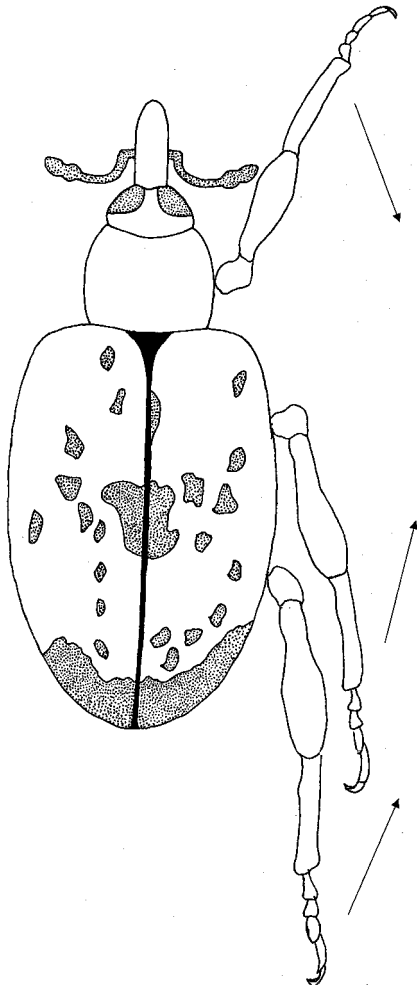


Fig. 4. First phase of the recovery stroke as indicated by the extension and retraction of the prothoracic legs. Arrows indicate the direction the legs are moving as the phase progresses. Legs are shown disarticulated from the body to illustrate the position of the coxae.

Analysis of the excised legs of all three species of *Hypera* (*H. eximia* – swimming, *H. postica* – nonswimming, *H. nigrirostris* – nonswimming) showed only slight variation among species and no apparent variation among generations within each species in terms of external morphology (Fig. 6). However, statistical analysis of measurements taken from each of the four leg segments (femur, tibia, tarsus, and tarsal claw) revealed significant differences among species that support our previous assignment of specific roles to each of the pairs of legs while swimming.

The prothoracic legs of *H. eximia* have significantly longer femora, tibiae, and significantly wider tarsi when compared with the two nonswimming species. Clearly, the increased femoral and tibial length is important in orientation of movement since extirpation of the prothoracic legs caused the weevil to lose its capacity to control its direction during swimming.

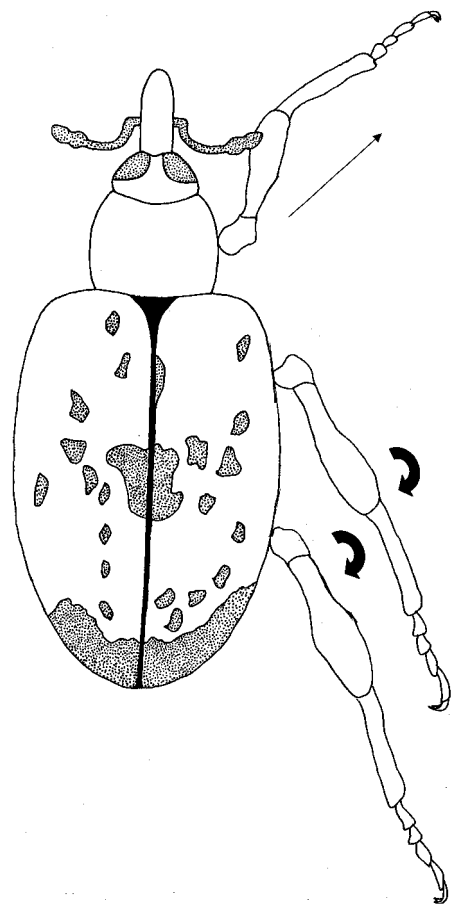


Fig. 5. Second phase of the recovery stroke as indicated by the retraction of the meso- and metathoracic legs. Arrows indicate the direction the legs are moving as the phase progresses. Legs are shown disarticulated from the body to illustrate the position of the coxae.

Increased tarsal width is also important because it provides the additional surface area at the tip of the limb required to produce the initial direction change efficiently while also stabilizing the weevil and preventing it from breaking the anterior surface tension and sinking.

Examination of the mesothoracic legs showed a similar pattern of increased femoral length, tibial length, and tarsal width in *H. eximia*. However, the mesothoracic legs had significantly increased width in the femur as well. Extirpation of the mesothoracic legs led to an immediate loss of stabilization during the power and recovery strokes, as well as a loss in overall propulsion. This suggests that, just as in the prothoracic legs, the increased femoral length, tibial length, and tarsal width are necessary to stabilize the weevil and prevent rolling while swimming (a commonality with all asynchronous swimming behaviors). However, extirpation also caused a reduction in the weevil's propulsion ability suggesting an additional role of the mesothoracic legs in thrust during swimming.

Table 1. Mean measurements of the four leg segments in each *Hypera* species

Characters	<i>H. eximia</i>			<i>H. postica</i>			<i>H. nigrastrus</i>		
	Pro	Meso	Meta	Pro	Meso	Meta	Pro	Meso	Meta
Femur length	1.40a	1.45a	1.51a	1.17b	1.17b	1.34b	1.13b	1.16b	1.28b
Femur width	0.41a	0.39a	0.39a	0.39ab	0.35b	0.34b	0.37b	0.34b	0.35b
Tibia length	1.28a	1.17a	1.34a	1.06b	0.96b	1.24a	0.99b	0.89b	1.19a
Tibia width	0.19a	0.19a	0.19a	0.17b	0.17b	0.16b	0.16b	0.16b	0.17b
Tarsal length	0.84a	0.82a	0.88a	0.66b	0.64b	0.80a	0.76a	0.71b	0.83a
Tarsal width	0.15a	0.12a	0.13a	0.12b	0.11b	0.12b	0.12b	0.10b	0.11b
TC length	0.42a	0.39a	0.42a	0.36b	0.35a	0.39a	0.37b	0.37a	0.38a
TC width	0.10a	0.10a	0.10a	0.09b	0.08b	0.09b	0.08b	0.08b	0.08c
Femur L/W ratio	3.39a	3.70a	3.86ab	3.04b	3.37b	3.92a	3.09b	3.30b	3.66b
Tibia L/W ratio	6.77a	6.18a	7.25a	6.07b	5.67ab	7.46a	6.06b	5.54b	7.01a
Tarsal L/W ratio	5.79a	6.63a	6.90b	5.80a	5.99b	6.99b	6.53a	6.84a	7.79a
TC L/W ratio	4.23a	4.11b	4.04b	4.29a	4.20b	4.50b	4.44a	4.76a	5.04a

Lowercase letters indicate significant differences within the same row.

The metathoracic legs were only different among species in terms of femoral width. This would seem contrary to providing additional surface area to contact the water and generate the propulsion needed for directed movement. However, the increased femoral width is likely to be directly related to the weevil's ability to propel itself forward in the water. Extirpation of the metathoracic legs resulted in a substantial loss of thrust, but no other significant differences could be identified suggesting no other obvious role in swimming for the metathoracic legs besides thrust.

Further examination of the length/width ratios for each of the leg segments revealed patterns that support the roles of each leg pair described above. In the prothoracic legs, it is important to maintain femoral and tibial length-width ratios of >3.1 and >6.5 , respectively. Similarly, the mesothoracic legs need to have femoral and tibial ratios of >3.6 and >6.0 , respectively, for proper stability and propulsion. However, no such pattern exists for any of the leg segments of the metathoracic legs, suggesting that all three species have sufficient means for propulsion. However, since only *H. eximia* has developed the behavioral modifications necessary to swim, it is likely that the orientation and the stabilization roles assigned to the prothoracic and mesothoracic legs are more important in successful surface swimming. The prothoracic and mesothoracic leg ratios, mentioned above, also provide a means of identifying potential swimmers among other *Hypera* species.

Discussion

Of the three weevil species studied, only *H. eximia* exhibits swimming behavior of any kind. This behavior is unique from other swimming species in the Curculionidae (Hix et al. 2000), though it appears to be similar with other *Hypera* species (Read 1982). The breaststroke-swimming style is denoted by a definitive power and recovery stroke. These strokes are both diphasic with a resting phase between them. During these phases the legs are held in definitive positions. These positions are extremely important due to the physical forces the weevils experience, especially drag, surface tension, yaw, rolling, and pitch. During

the diphasic-power stroke, the legs are extended to their maximum length laterally with the most area in contact with the water, and move with the greatest velocity of any phase. The tarsi also are outstretched laterally from the tibia. This is important, because the thrust that a leg exerts in water is proportional to its area and the square of the velocity with which it moves. Further, higher speeds can be produced if the greatest surface area is farthest from the body (Chapman 1998). Induced drag, caused by the submerged rostrum, is likely to reduce the maximum speed attained by the weevil. However, the rostrum imparts stability and directionality. By remaining in contact with the water surface during forward momentum, the rostrum reduces yaw, or side-to-side motion, of the anterior portion of the beetle. The rostrum also acts to provide the weevil with a means for turning. Other swimming weevils accomplish turning by performing unequal stroke frequency on opposing sides of the body (Hix et al. 2000). Therefore, the turning mechanism of *H. eximia* is also a unique behavior among Curculionidae. Rolling and pitching are controlled by the mantis-like position of the forelegs during the power stroke and the outstretched pro-, meso-, and metathoracic legs during the recovery stroke.

Morphometric analysis of the leg segments of all three species showed differences which confirm that leg morphology supports the behaviors employed by *H. eximia* that contribute to its ability to swim, while congeners flounder. It has been shown that minor variations in morphology can have profound effects on the efficiency of locomotion (Evans 1985, Ribera and Isart 1991, Bilton 1993, Ribera and Nilsson 1995). To better understand the role that each pair of legs plays behaviorally and morphologically, it is easiest to analogize *H. eximia*'s surface swimming to the design and motion of a boat with oars and a prop. The prothoracic legs and rostrum act as anteriorly directed "rudders" that extend laterally from the body and allow for multidirectional orientation, as well as providing some measure of anterior stability during sharp turns. The mesothoracic legs can be thought of as a middle row of oarsmen who not only provide some thrust, but also help to keep the boat balanced while the primary

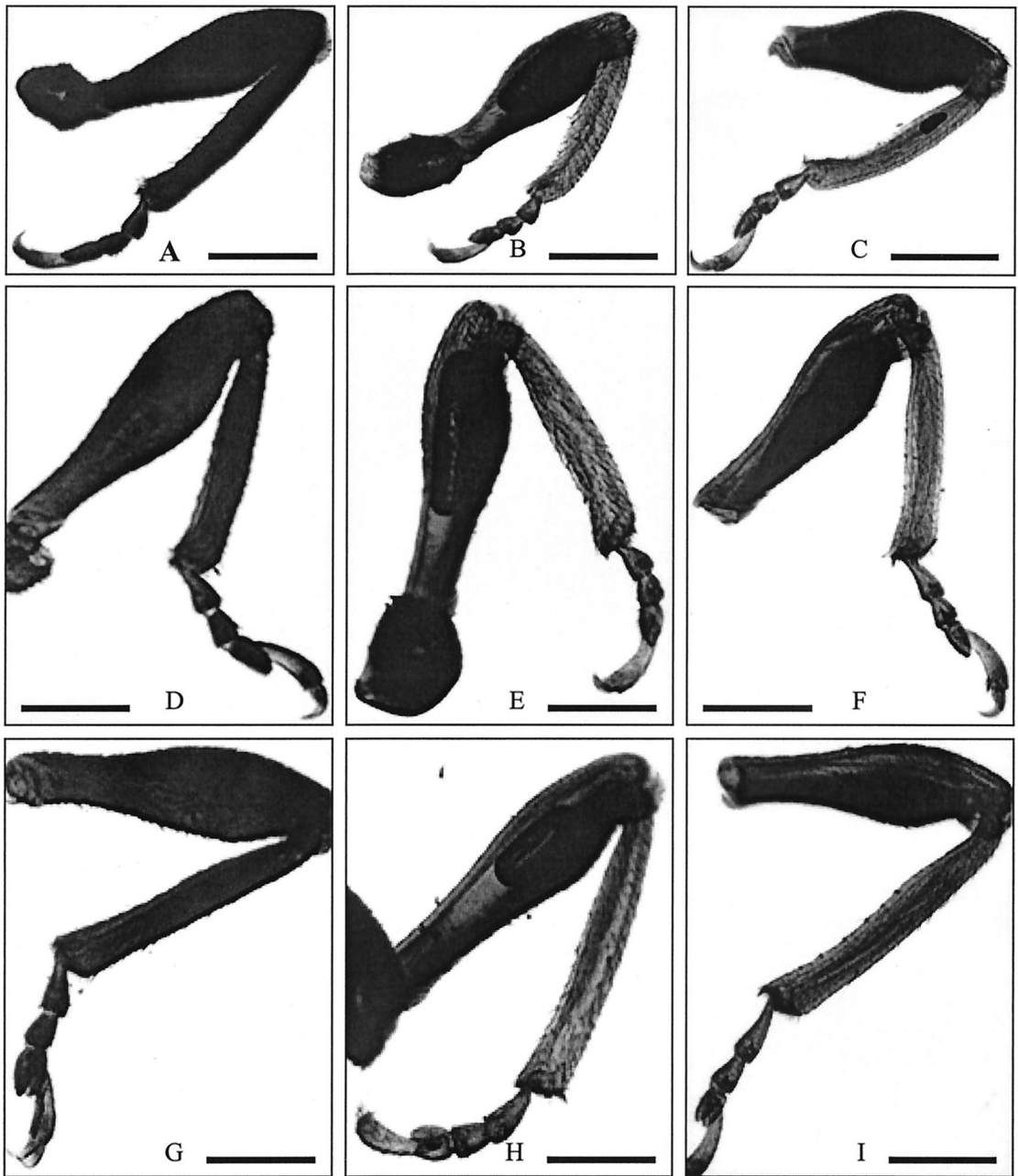


Fig. 6. Pro-, meso-, and metathoracic legs of *Hypera* species (4 \times). (A) *H. eximia*, prothoracic leg. (B) *H. postica*, prothoracic leg. (C) *H. nigrirostris*, prothoracic leg. (D) *H. eximia*, mesothoracic leg. (E) *H. postica*, mesothoracic leg. (F) *H. nigrirostris*, mesothoracic leg. (G) *H. eximia*, metathoracic leg. (H) *H. postica*, metathoracic leg. (I) *H. nigrirostris*, metathoracic leg. Lines represent 0.5 mm.

thrust comes from the metathoracic legs acting as a propeller.

The increased femur width in the mesothoracic and metathoracic legs is likely due to enlargement of the tibial muscle insertions. This type of musculature arrangement can be found in other insects, such as Orthoptera, where the tibial muscles provide the

power for jumping (Schmidt-Nielson 1972, Pflüger and Burrows 1978). However, in the case of *H. eximia*, the motion is not dorso-ventral (as it would be in jumping). Instead, the motion is directed antero-posteriorly providing the weevil with both primary and secondary propulsion, depending on which leg pair is involved.

The breast-stroke swimming behavior of *H. eximia* is suggestive of an independent phylogenetic origin for swimming in the Curculionoidea, specifically within the curculionid subfamily Hyperinae. Before this description, swimming in the Curculionoidea was restricted to the Eriirhinidae (*Lissorhoptrus*), the Dryophthoridae Rhyncophorinae (*Sitophilus*), and the Curculionidae Bagoniinae (*Bagous*), Ceutorhynchinae (*Poophagus*, *Eubrychius*, *Phytobius*, and *Euhrychopsis*), Molytinae (*Conotrachelus*). The evolution of swimming in Hyperinae is of independent origin, due to the phylogenetic placement of the subfamily. This newly reported swimming behavior increases the number of swimming modes exhibited by weevils from three to four.

The surface swimming of *H. eximia*, discussed herein, represents the first documented account of swimming behavior in this species. Surface and subsurface swimming are also exhibited by *Bagous cavifrons* (LeConte), *Eubrychius velutus* Beck, and *Poophagus symbrii* (F.) (Morris 1976, O'Brien and Marshall 1979). The former two species are excellent subsurface swimmers and the latter a surface skater. The use of morphometric analysis, time-lapse videography, and extirpation experiments is useful for offering detailed descriptions of the behavioral and morphological adaptations of the species and how those characters contribute to each of the patterns required for coordinated movement (Daly 1985). This type of multifaceted approach is necessary for understanding how, *H. eximia*, *H. rumicoides*, *H. compta*, *H. rumicoides*, and *H. paludicola* have developed the capacity to swim while other *Hypera* spp. have not. Further studies with members of this subfamily are essential for understanding the evolution of swimming in the Curculionoidea.

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