


Tiger Beetles of Manitoba: Ecology, Life History and Microsculpture

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Front cover images:
Big Sand Tiger Beetle adult (Larry de March)
Laurentian Tiger Beetle head (Larry de March)
Oblique-lined Tiger Beetle larva (Deanna Dodgson)
Laurentian Tiger Beetle head SEM (Erwin Huebner)

Back cover image:
Bronzed Tiger Beetle devouring a spider (Larry de March)

DEDICATION

The author dedicates this book to the following cicindelophiles of the past for their years of dedicated research and reporting on Manitoba's tiger beetles:

Thomas Say
Norman Criddle
John Braithwaite Wallis
Colin Hawkins
Dr. William B. Preston

”There is no service of greater value to a field student than that which arises when a resident scientist shows a visitor communities with which he is unfamiliar.”
Victor E. Shelford (The Ecology of North America, 1963)

“It is my firm belief that one beginning the study of ecology should first of all become thoroughly acquainted with the places animals may be found in nature, what kinds of organisms occur in different habitats, the abundance and interrelations of organisms in these habitats, the behavior and the life requirements of the principal species, and the structure and succession of communities.”
S. Charles Kendeigh (Animal Ecology, 1961)
The author's ecology mentor at the University of Illinois, Urbana–Champaign

“Types of Familiar Insects – Bees, Humblebees, Flies, Etc.”
Note the three species of tiger beetles in the lower-left corner. (Hazlitt Alva Cuppy, 1895. Beauties and Wonders of Land and Sea: A Book on Natural History)

Purple (Cowpath) Tiger Beetle (*Cicindela purpurea*). “Small animal life within and upon the North American Forest Floor.” (Walter Linsenmaier, 1972. Insects of the World). With permission from Ms. Maja Linsenmaier.

In his 1982 classic book, "Beetles," Bernhard Klausnitzer asked; "Why ever should there be yet another book on beetles? There are, after all, so many already and new ones keep appearing! But let us hope that in the future too, new books on this subject will continue to be written and printed, and it is quite certain that they will always find interested readers. For there is an endless fascination in recounting the great variety within this group of animals, in selecting features peculiar to them, in depicting for the nature-lover the fascinating beauty of beetles..."

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TIGER BEETLES OF MANITOBA: ECOLOGY, LIFE HISTORY AND MICROSCULPTURE

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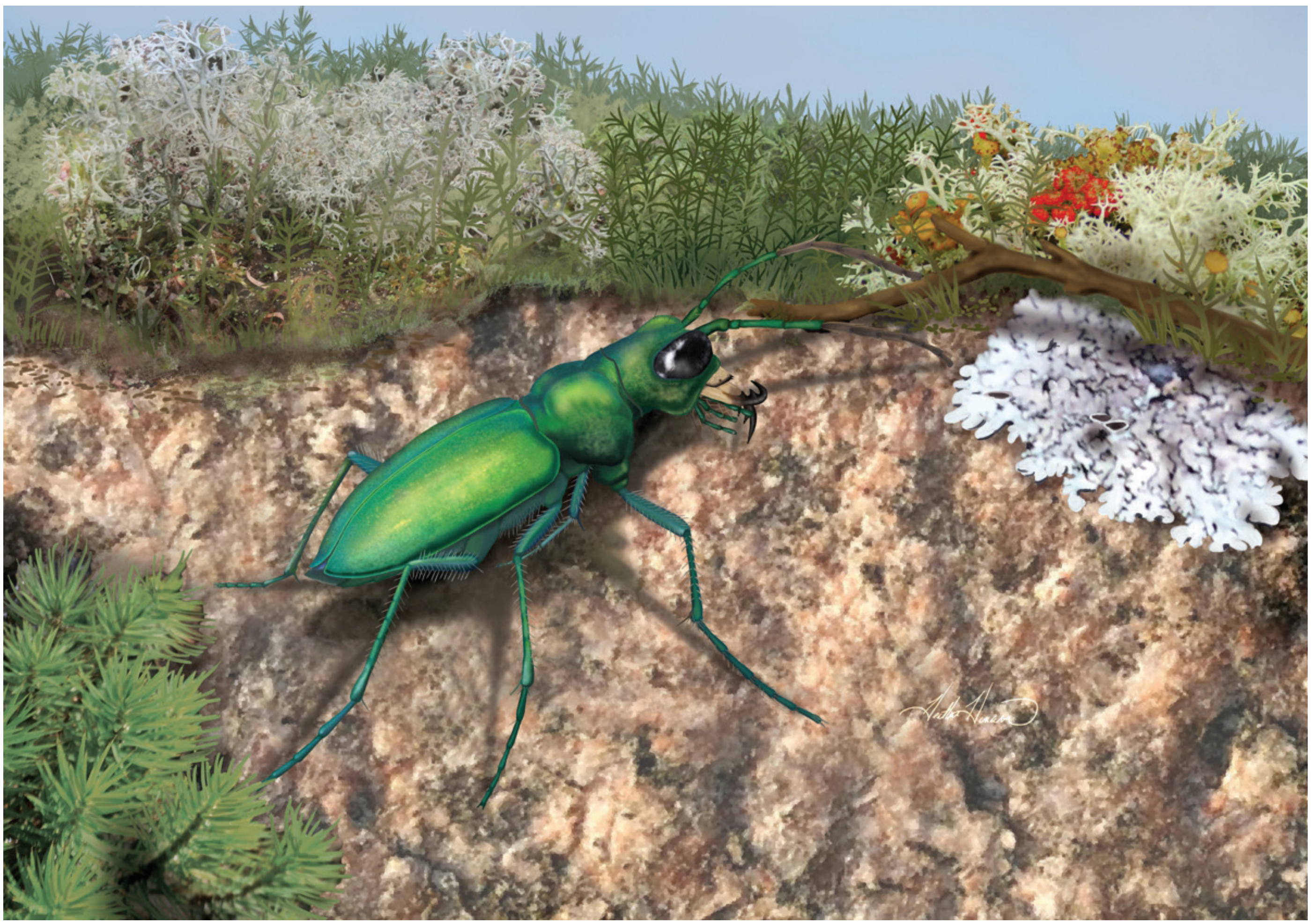
INTRODUCTION

Tiger beetles (family *Cicindelidae*) are highly active and elusive insects named for their voracity as predators. With keen eyesight and tracking skill, they run down moving prey and strike with lightning speed, piercing their victims repeatedly with their prominent, canine-like, multi-toothed mandibles. Another major reason for these beetles' success is their ability to exploit challenging habitats (e.g., saline mudflats and sand dunes) shunned by many other kinds of insects. They vary considerably in size from the delicately formed, 7-mm Little Tiger Beetles (*Brasiella* species) occurring from the southern United States to South America, and the 36-mm *Amblycheila* species of the United States and Mexico, to the robust, 70-mm Manticore Tiger Beetles (*Manticora* species) of southern Africa (see bronzes in chapter on Tiger Beetles as Models). Females are generally slightly larger and broader than males. All Manitoba species are capable of rapid flight.

A total of 19 species has been reported in Manitoba. Many are beautifully coloured, often with metallic reflections, featuring distinctive and complex, camouflaging patterns on their wing covers. The array of colours arising from all aspects of the body results from the presence of pigment (such as melanin), lipids and translucent waxes, and from the reflection and refraction of light (i.e., structural colour) derived from the multiple layers forming the hard cuticle. Duran et al. (2020) stated that; "Tiger beetle colours originate from a series of thin epicuticular sheets, which act as a multilayer interference reflector. Thin layers of melanin alternate with translucent layers, and the distance between the melanin layers determines the primary wavelengths reflected." Shelford (1917) demonstrated in laboratory experiments that dorsal colour is partly determined by developmental conditions during pupation. Colours, patterns, and surface textures (e.g., shiny, dull, granular, pitted) are important factors for identification of species and subspecies.

Tiger beetles also demonstrate fascinating ecological relationships and complex life-history traits, and consequently, they have attracted the keen interest of professional and amateur entomologists for well over a century. Vernon Kellogg (1914) noted that; "The attractive tiger-beetles (*Cicindelidae*) are great favorites with collectors, and deservedly. Their vivid, sharply marked metallic colors, trim clean body, and constant alertness and activity, together with their fondness for warm, bright hunting grounds and their clever and "gamy" elusiveness of the collecting-net, combine to give these fierce, swift little creatures a high place in the regard of the beetle-catching sportsman." Pearson et al. (2015) concluded that; "Detailed study of their natural history, population dynamics, communities, patterns of worldwide species richness, and taxonomy of particular subgroups have produced much information. Tiger beetles, as a result, are among the most widely investigated groups of insects, especially in terms of their ecology and geographic distribution." Many excellent photographs of tiger beetles are available on the internet.

Most North American species of tiger beetles are observed standing or running on bare substrates on warm sunny days, although the coloured Metallic (*Tetracha* species), black Night-stalking (*Omus* species), and black Giant (*Amblycheila* species) tiger beetles are nocturnal. Species typically demonstrate narrow or wide preferences for specific types of substrate, soil moisture, and exposure, such as barren sand dunes, sandy or muddy shorelines, clay banks, saline or alkaline clay flats, grassland with open spaces, sun-dappled forest paths, exposed rock outcrops, and gravel deposits. Manitoba tiger beetles exploit these open, sparsely vegetated habitats -- ones that many other species of beetles avoid, thereby avoiding competition. Certain tropical species restrict their hunting activities to tree trunks or leaves. Most species inhabit early successional plant communities and disturbed habitats, which the beetles are quick to discover through their great mobility – running and flying, sometimes assisted by strong winds (Graves 1963). Pearson et al. (1997) described 17 habitat types utilized by tiger beetles in the United States and Canada, and found that the majority of species are found in only one habitat. A few species, such as *Cicindela tranquebarica*, occur in up to six types. This species demonstrated the widest range of habitats in Manitoba, and the third-largest range, while *Ellipsoptera lepida* is an example of a Manitoba species present in only a single habitat – active sand dunes – and with the small population isolated in the Carberry Sandhills.



The Laurentian Tiger Beetle stationed on its typical habitat of a Precambrian Shield rock exposure, waiting to detect and track down passing prey. (© Heather Hinam)

Although several other provinces (e.g., Acorn 2001, for Alberta) and states (e.g., Knisley and Schultz 1997, covering the South Atlantic states) have produced publications or annotated lists of tiger beetles for their jurisdictions, none has appeared on the tiger beetles of Manitoba, save for Norman Criddle's three brief, but enlightening, early papers (1907, 1910, 1915) on the habits of most local species. Manitoban J. B. Wallis published "The Cicindelidae of Canada" in

1961, which included the records and habitats of the species found in Manitoba, however much additional information has been acquired through the field activities of several researchers since 1970.

The most-comprehensive source of current information on Manitoba and North American species is by Pearson et al. (2015). Other excellent guides are by Willis (1967), Pearson (1988), Graves and Brzoska (1991), Leonard and Bell (1999), Acorn (2001), Pearson and Vogler (2001), Choate (2003), Spomer et al. (2008), Brust and Reese (2020), and Beaton, Krotzer and Holt (2021). Beginning in 1969, Ronald L. Huber of Minnesota has continued to publish the quarterly journal *Cicindela*, which considers tiger beetle ecology, life history, conservation status, morphology, and taxonomy of tiger beetles on a world-wide basis. His knowledge of tiger beetles, and his long-term dedication to promoting research and publication on these insects, are truly remarkable.

Detailed distribution maps and lists of locality data for Manitoba species of tiger beetles are being published elsewhere.

OBJECTIVES

The objectives of this study are to:
- provide a summary of the group's ecology, life history, and behaviour, based on the author's observations and those reported in the literature,
- reveal the breathtaking microsculpture of selected species of Manitoba tiger beetles, and
- encourage others to undertake observations and ecological studies of these fascinating insects.

CHECKLIST OF MANITOBA TIGER BEETLES (SPECIES AND SUBSPECIES) (Bousquet et al. 2013)

Laurentian Tiger Beetle, *Cicindela denikei* W.J. Brown, 1934
Twelve-spotted Tiger Beetle, *Cicindela duodecimguttata* Dejean, 1825
Big Sand Tiger Beetle, *Cicindela formosa generosa* Dejean, 1831
Crimson Saltflat Tiger Beetle, *Cicindela fulgida fulgida* Say, 1823
Crimson Saltflat Tiger Beetle, *Cicindela fulgida westbournei* Calder, 1922
Hairy-necked Tiger Beetle, *Cicindela hirticollis shelfordi* Graves, 1988
Blowout Tiger Beetle, *Cicindela lengi versuta* Casey, 1913
Common Claybank Tiger Beetle, *Cicindela limbalis* Klug, 1834
Sandy Tiger Beetle, *Cicindela limbata hyperborea* LeConte, 1863
Sandy Tiger Beetle, *Cicindela limbata nympha* Casey, 1913
Long-lipped Tiger Beetle, *Cicindela longilabris longilabris* Say, 1824
Prairie Long-lipped Tiger Beetle, *Cicindela nebraskana* Casey, 1909
Cow Path Tiger Beetle, *Cicindela purpurea audubonii* Leconte, 1845
Cow Path Tiger Beetle, *Cicindela purpurea purpurea* Olivier, 1790
Bronzed Tiger Beetle, *Cicindela repanda repanda* Dejean, 1825
Festive Tiger Beetle, *Cicindela scutellaris lecontei* Halderman, 1853
Oblique-lined Tiger Beetle, *Cicindela tranquebarica kirbyi* Leconte, 1867
Oblique-lined Tiger Beetle, *Cicindela tranquebarica tranquebarica* Herbst, 1806
Punctured Tiger Beetle, *Cicindelidia punctulata punctulata* Olivier, 1790
Coppery Tiger Beetle, *Ellipsoptera cuprascens* (LeConte, 1852)
Ghost Tiger Beetle, *Ellipsoptera lepida* (Dejean, 1831)
Nevada Tiger Beetle, *Ellipsoptera nevadica knausii* (Leng, 1902)
Variable Tiger Beetle, Parvindela (*Cylindera*) *terricola cinctipennis* (LeConte, 1846)
Variable Tiger Beetle, Parvindela (*Cylindera*) *terricola terricola* (Say, 1824)
19 species, 24 taxa

METHODS

The results presented in this study are derived from countless field trips conducted around the province by Wrigley and de March, and other researchers past and present, covering a period of 115 years (see Norman Criddle's publications). Roads, trails and satellite images were searched for possible sites of populations of tiger beetles, and thousands of voucher specimens were collected and photographed in documenting the presence of species. Specimens were collected using aerial insect nets, occasionally by hand, and sometimes picked up dead on the ground, or from under rocks and other debris. Manitoba tiger beetles have been deposited in a number of museums and collections, predominantly in the following:

- J.B. Wallis/R.E. Roughley Museum of Entomology, University of Manitoba, Winnipeg
- Manitoba Museum, Winnipeg
- Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa
- Royal Ontario Museum, Toronto
- Canadian Museum of Nature (Ottawa)
- E.H. Strickland Entomological Museum, University of Alberta, Edmonton
- Spencer Entomological Collection, Beaty Biodiversity Museum, University of British Columbia, Vancouver

TIGER BEETLE RESEARCHERS IN MANITOBA

Thomas Say (1787-1834), revered as the 'Father of American Descriptive Entomology,' was likely the first naturalist to record and collect tiger beetles in the Manitoba region when he was appointed Zoologist for Major S. H. Long's expeditions to St. Peters River, Lake Winnipeg, and Lake of the Woods in 1823 (Keating 1924). His 1817 book on American Entomology illustrated tiger beetles (plate 6), including *Cicindela formosa,* and in 1818, he published a monograph on North American tiger beetles of the genus *Cicindela*.

Norman Criddle (1875-1933) was the first naturalist to focus studies on Manitoba tiger beetles, with many years of observations centered in the vicinity of his home entomology lab at a site called Aweme (49.70875N, 99.60202W), on the southwest corner of the Carberry Sandhills. His remarkably detailed studies on tiger beetle life history were summarized in three publications appearing in The Canadian Naturalist in 1907, 1910 and 1915.

John Braithwaite Wallis (1877-1961) was a Manitoba school teacher and principal who made a major contribution to Manitoba and Canadian entomology, culminating in his 1961 book; "The Cicindelidae of Canada," which included distribution maps, taxonomic evaluations, and ecological notes on 19 Manitoba species of tiger beetles. Dr. George Ball (Chairman, Entomology Department, University of Alberta) finalized the manuscript and saw it through to publication, since J.B. Wallis was in ill health and passed away soon after (Acorn 2001).

Dr. William B. Preston (1937-2013) began collecting tiger beetles and other insects in Manitoba shortly after he arrived in Winnipeg in 1969, to take up a curatorial position (responsible for studying amphibians, reptiles, fishes, and arthropods) at the new Manitoba Museum of Man and Nature. Collecting tiger beetles for many years, he prepared an early draft of species accounts, beetle-activity charts, and distribution maps for a planned paper on Manitoba tiger beetles. Unfortunately he was unable to complete it. His large collection of insects was donated to the J.B. Wallis/R.E. Roughley Museum of Entomology.

Amateur entomologist Colin Hawkins (1942-1999), of Rapid City, Manitoba, was a keen collector of insects in southwestern Manitoba, specializing in tiger beetles and hawkmoths, and 'swapped' numerous specimens with other collectors worldwide. Colin extended the ranges of a number of insects including *Cicindela fulgida westbournei* and *Parvindela terricola*. His collection of beetles was acquired by the author, who will eventually place these specimens in the J.B. Wallis/R.E. Roughley Museum of Entomology.

Todd Lawton researched tiger beetles from 1985 to 2020, collected extensively throughout Manitoba, Canada, and the United States, and amassed a collection of over 22,000 specimens. From 2002-2019, he travelled to remote northern areas of Manitoba and Saskatchewan (regions having received minimal investigation), and recorded major range extensions, and maculation and colour variations, for 13 species of tiger beetles (Lawton 2018). He continues to donate specimens to several museums.

The author, Dr. Robert E. Wrigley, is a retired mammalian ecologist, and former Manitoba Museum Curator (Birds and Mammals) and Museum Director, Founding Director of the Oak Hammock Marsh Interpretive Centre, and later Curator of the Assiniboine Park Zoo. He was introduced to tiger beetles in the mid-1970s by Drs. Bill Preston and Brian McKillop (both former Curators at the Manitoba Museum), and has researched tiger beetles in Manitoba and United States periodically from 1994 to 2020. He has donated hundreds of tiger beetle specimens mainly to the J.B. Wallis/R.E. Roughley Museum of Entomology, and the Canadian National Collection of Insects, Arachnids and Nematodes. He maintains a personal, world-wide collection of 230 species of tiger beetles, and over 10,000 species of coleoptera.

Larry de March is a retired biologist, formerly a Director of Resource Management with Fisheries and Oceans Canada. Always interested in nature, he photographs wildlife and studies the distribution of tiger beetles, odonates, and wildflowers.

Other local and visiting amateur and professional entomologists have sampled insects in Manitoba, and consequently tiger beetle specimens are represented in a number of major museum and private collections in North America and Europe.

CLASSIFICATION

The genus *Cicindela*, the basis for the family name, Cicindelidae, was described by Carolus Linnaeus in 1735 (Leng 1902). He was familiar with nine species of tiger beetles at the time, three of which he had collected earlier as a university student on a field expedition to Lapland (Pearson and Vogler 2007). The name *Cicindela* is drawn from the Latin ‘cicindel,’ a glow worm, perhaps referring to the worm-like larva of tiger beetles. The name ‘beetle’ derives from the Middle English words ‘bityl’ or ‘betyll,’ meaning ‘little biter,’ while ‘tiger’ obviously refers to the impressive biting mandibles typical of these insects. Tiger beetles have traditionally been placed in their own family, Cicindelidae Latreille, 1804 (e.g., Crowson 1981, Freitag 1999, Pearson and Vogler 2001, Knisley and Gwiazdowsli 2020, Duran and Gough 2020), however the group is recognized by some entomologists as a subfamily, Cicindelinae, of the ground beetle family Carabidae, within the Suborder Adephaga (e.g., Bousquet et al. 2013). Putchkov and Cassola (2005) described morphological characters of both larval and adult tiger beetles that distinguished the taxon from Carabidae, thus supporting distinct family status for Cicindelidae. Common names of tiger beetles inhabiting the United States and Canada were officially designated in a paper by Richard Freitag (1999).

But we’ve always been known as the Cicindelidae family! I have documents to prove it.
(cartoon Rob Gillespie; concept Robert Wrigley)

The Cicindelidae taxon is distinguished from ground beetles (Carabidae) by:
-long, sickle-shaped mandibles demonstrating left-dominant mandibular chirality (larger left mandible), with simple teeth arranged along the inner side, and a compound, molar-like tooth on the inner base (Brust and Hoback 2016),
-pair of large bulbous eyes in the adult (two pairs in the larva), which offer excellent vision,
-pair of thin, 11-segmented antennae with insertions on the frons (forehead), between the bases of the mandibles, in front of the eyes,
-clypeus (sclerite on the lower margin of the face) widened and extending beyond the antennal insertion on both sides,
-long body with head (including eyes) wider than the thorax,
-long, thin running legs with abundant setae, and
-tunnel-building larvae featuring an enlarged fifth abdominal segment armed with two pairs of forward-facing hooks and bristles, which help keep the larva anchored in the burrow. (Pearson and Vogler 2001; Pearson et al. 2015, Brust and Hoback 2016).

Certain other levels of classification of tiger beetles have proven controversial for over a century. Several Manitoba species formerly included in the genus *Cicindela* have recently been given their own generic name (e.g., *Cicindelidia punctulata, Parvindela* (*Cylindera*) *terricola, Ellipsoptera lepida*). Many tiger beetles demonstrate significant variation over their ranges, and multiple populations have been given formal subspecific names. Due to significant overlap in morphological and colour characteristics in some species (e.g., *C. nebraskana* and *C. longilabris*), there has been debate on their taxonomic status, whether they represent full species, hybrids, or clinal variation (Spomer 2009). The incorporation of data from DNA research (e.g., Vogler and Welsh 1997, Knisley et al. 2008), multilocus nuclear analysis (Duran et al. 2020), and horizontal starch-gel electrophoresis (Foster and Knowles 1990) are clarifying the phylogeny and status of challenging cicindelid taxa. New cryptic species (i.e., a former species that is determined to be two or more similar species) are being increasingly found with new diagnostic techniques.

Interestingly, cicindelids demonstrate the most-ancient multiple-X chromosomal system known (2-4 X chromosomes plus Y), and most North America species have the ancestral XXXY complement. Three Manitoba *Cicindela* species revealed a formula of 9+3XY, *Cicindelida punctulata* 9+3XY, *Cylindera* (*Parvindela*) 9+3XY or 9+4XY, and *Ellipsoptera* 9+4XY. Rearrangements of genes are thought to increase genetic variation among populations and to restrict reproductive compatibility, thereby favouring reproductive isolation of populations (Galian et al. 2007).

COMPARISON OF MANITOBA'S TIGER BEETLE FAUNA WITH OTHER JURISDICTIONS

Blatchley (1910) stated that 1400 species of cicindelids were known throughout the world at the time, with 93 species recorded for the United States. Over 2800 species have now been described to date (within 108 genera), with representation ranging from tropical, temperate and boreal regions, including all continents except Antartica (carabidae.org Cicindelinae). Currently, 118 species have been documented within the United States and Canada, with 153 recognized subspecies (Pearson et al. 2015, Duran and Roman 2019). Canada lists 29 species (Bousquet et al. 2013), 19 of which have been recorded during historic times in Manitoba. A hypothetical species for the province is the Cream-edged Tiger Beetle (*Eunota circumpicta pembina*), which has been collected by the author and others, just east of Hamilton, North Dakota, only 20 km south of the Manitoba border; suitable patches of saline habitat occur in between. This limited population, existing on a few disjunct salt flats south to Grand Forks (Willis 1967), is separated by 800 km to the main range in Nebraska (Pearson et al. 2015). It is a prime example of a relict population, left behind when the main range of the species shifted far to the south following the warm-dry (Mid-Holocene) period 6000 years ago (https://www.ncdc.noaa.gov/global-warming/mid-holocene-warm-period). It is quite possible that it occurred on the Manitoba side of the border (where suitable habitat even now exists), when the climate was significantly warmer and drier than at present.

For comparison, Saskatchewan hosts 19 species, Alberta 18, British Columbia 13, Ontario 16, Quebec 14, Minnesota 21 (R. Huber pers. comm.), North Dakota 22 (Patrick Beauzay, pers. comm., Larson 1981), South Dakota 24 or 25 (Kirk and Balsbaugh 1975, Spomer et al. 2008), and Nebraska 32 (Spomer et al. 2008). Arizona and Texas have the largest tiger beetle faunas in North America, north of Mexico, with 37 and 35 species, respectively. A recent tally lists 116 species in Mexico (http://www.cicindelaonline.com/index.htm). Other major regions with exceptionally high diversities of tiger beetles are the Malay Archipelago 449, South America 419, Africa 401, and the Indian subcontinent 296 (Pearson and Vogler 2001). These data demonstrate a universal pattern in animal and plant species abundance -- latitudinal and altitudinal gradients in richness toward the tropics. Numerous factors have been proposed to explain these phenomena, including original lineage size, greater solar radiation, less fluctuation in annual temperatures, habitat complexity, longer growing season, and lack of paleoclimatic perturbations such as glaciations (Pianka 1966, Pearson and Vogler 2001).

SPECIES DISTRIBUTIONS PAST AND PRESENT

Tiger beetles are believed to have evolved around 200 million years ago, possibly on what is now the African continent, and eventually attained a cosmopolitan distribution (Mandl 1954, Pearson and Vogler 2001). Although rarely appearing in the fossil record due to their delicate morphology, tiger beetle elytra and mandibles have been identified dating back to the Early Cretaceous Period, 125 million years ago, with the oldest-known species being *Cretotetracha grandis* from deposits of the Yixian Formation, Yangshuwanzi, China (Zhao et al. 2019). Other Mesozoic fossil tiger beetles, including *Oxycheilopsis cretacicus,* have been described from the Crato and Santana formations of Brazil, dated 113 million years ago (Gough et al. 2018). Horn (1876) discussed two fossil species of *Cicindela* from a post-Pliocene cave in Pennsylvania. Nagano et al. (1982) summarized the few North American fossil records, which included a *Cicindela sexguttata* specimen from Minnesota (dated 12,400 BP) and *C. repanda* and *C. limbalis* from southern Ontario, of approximately the same post-Wisconsinan glacial age. Future studies of fossilized insects in Manitoba deposits may turn up evidence of invasions of tiger beetles into the southern region of the province during interglacial warm periods (interstadials) of the Quaternary (2.6 million years ago to the present).

Manitoba was entirely repeatedly blanketed (to a depth of over 1.6 km) and scoured by the Laurentide Glacier as recently as 12,000 years ago, and then mostly inundated by Glacial Lake Agassiz from 11,500 to 9,000 years ago. Biological communities began to return to southern

Manitoba once dry land emerged in the southwest corner around 9,000 years ago. A succession of tundra and spruce-lichen woodland was followed by a rapid expansion of grassland, which reached farther north than at the present time around 5,000 years ago (Shay 1984). The current ranges of tiger beetles in Manitoba should therefore be interpreted as mobile phenomena, with the currently boreal-distributed species (e.g., *C. tranquebarica*) presumably arriving before grassland species (e.g, *Cicindelidia punctulata*). A few species may be referred to as glacial relicts (e.g., *Ellipsoptera lepida*), occurring as isolated populations hundreds of kilometres from other populations to the south and west. Periods of drought, forest fires, and vast herds of large grazers such as Bison likely kept open patches of bare ground on the prairie and in forests, which would have provided habitats for populations of tiger beetles, just as Wood Bison herds do today west of Great Slave Lake in the Northwest Territories, along with drought and fire (Catling 2006).

On a shorter time scale, the author has observed instances where tiger beetles have been exceptionally abundant in a location for a number of years, and then vanished in succeeding years. As an example, one summer the author observed hundreds of *Cicindela fulgida westbournei* on roadside salt flats north of St. Laurent, Manitoba, followed by most years where not a single specimen could be located. Annual surveys often demonstrated wide fluctuations in most species' presence and abundance, even at the same time of year. Attempting to determine the factors influencing high or low populations from year to year is challenging, and sometimes appears attributable to weather conditions such as drought, flooding, a deep freeze, a failure of prey populations, or the rapid invasion of vegetative cover such as brome grass.

While certain species of tiger beetles, such as *Cicindela tranquebarica*, are found in a variety of habitats, others are entirely dependent on a specific type; for example, *Ellipsoptera lepida* on barren sand, and *Cicindela fulgida* on soil of high salt content. Consequently, the distributional patterns of the latter species are generally discontinuous, with often-small populations separated by great distances, and therefore susceptible to local extirpation. With the major loss of prairie, aspen parkland, and mixed-forest habitats to agriculture and other developments in southern Manitoba, many populations of tiger beetles have no doubt been reduced or eliminated within the last two centuries. *Cicindela hirticollis* is currently threatened due to its lake- and river- shoreline habitats and larval burrows being disturbed by human-related flooding, recreational use, and cottage development. *Cicindela denikei* and *Ellipsoptera lepida* are at risk due to their limited and peripheral distributions. Also, the control of natural prairie fires and the extermination of vast herds of grazing large mammals in the southern region of the province have permitted widespread plant succession (including many invasive plants) on formerly open sites, resulting in the attenuation and fragmentation of essential habitats for tiger beetles. The fact that most species of tiger beetles are habitat specific, and are subject to elimination from human-caused habitat disturbances, result in these beetles being selected as indicators of habitat quality. They may also demonstrate challenges due to climate change.

Species restricted to semi-open or barren sand-dune habitats, such as *Cicindela limbata nympha* and *Ellipsoptera lepida*, must now have greatly reduced populations and restricted distributions in Manitoba compared to the warm-dry period 6,000 to 3,000 years ago, when vast, barren dune fields existed in southern Manitoba following the retreat of the Laurentide ice sheet and the subsequent drainage of Glacial Lake Agassiz. With climate change, grassland and forest progressively invaded sandhills. The area of active sand dunes in Manitoba's largest dune field – the Brandon/ Carberry Sandhills – now occupies only 25 sq km, less than 5% of the contiguous sand deposit (Scott 1996), and has decreased by 50% since 1950 alone (Wolfe et al. 2000). Vast deposits of beach-ridge sand and glacial till, which would have offered habitat for several species of tiger beetles in the past, now lie under grassland and mixed and coniferous forest. Pearson and Vogler (2001) surmised that the decrease in active dune extent has resulted in the formation of five, now-isolated, subspecies of *Cicindela limbata,* ranging from northern Alaska and Manitoba to Nebraska. Remarkably, the Alaska subspecies, *C. limbata nogahabarensis,* is separated by 2600 km from the nearest population, *C. l. hyperborea*, to the southeast in the Northwest Territories (Pearson et al. 2015), evidence of a contiguous range in the past. The anticipated return of active, drifting sand in several Manitoba dune fields due to global warming in the future will likely reverse this trend of dune stabilization, and may encourage population expansion of tiger beetle species dependent on sandhills (Acorn 2011).

While tiger beetles have been studied for over a century in southern Manitoba, central and northern regions have received only minor attention, due to various logistical challenges. Northern Manitoba currently has 6 species of tiger beetles (*Cicindela longilabris, C.*

limbalis, C. limbata, C. tranquebarica, C. repanda and *C. duodecimguttata*), the central region has an additional 4 (*Parvindela terricola, Cicindela lengi, C. hirticollis*, and *C. purpurea*), while all 19 species have historically occurred in the extreme south of the province (pointed out by Todd Lawton, personal communication). *Cicindela longilabris longilabris* and *C. limbata hyperborea* are the northern-most species in Manitoba (Woodcock et al. 2010). The current author surmises that these species are prevented from extending further north, along the coast of Hudson Bay, by their larvae being unable to burrow into permafrost, and the decreasing period of summer warmth in which to feed.

Beach ridge near Churchill – the sandy habitat of both *C. longilabris longilabris* and *C. limbata hyperborea.* (© Robert Wrigley)

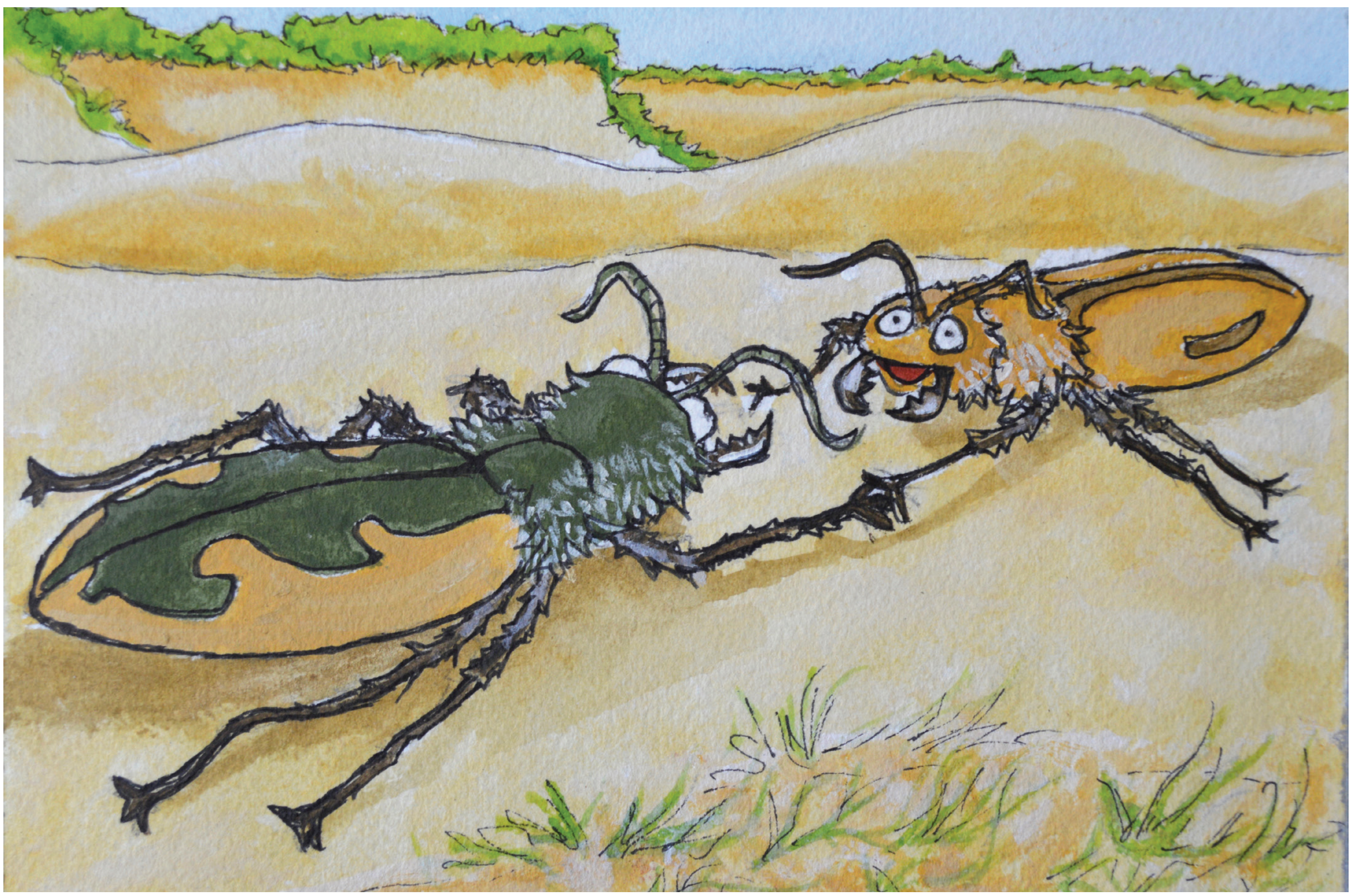
A few species may have taken advantage of human-caused dispersal routes, such as *Cicindela fulgida* and *Parvindela terricola*, extending their ranges northward by following highway ditches, where the original forest and grassland were replaced by low, salt-tolerant plants, kept patchy by annual spring flooding and the passage of snow machines in winter. Tiger beetles are remarkable for their dispersal abilities, with flight aided by wind, and consequently there are many extralimital records demonstrating this phenomenon (Pearson et al. 2015). Interestingly, certain ubiquitous species of tiger beetles, such as *Cicindela repanda* and *Cicindela tranquebarica*, are often quick to take advantage of new habitats created by human activities.

The Coppery Tiger Beetle (*Ellipsoptera cuprascens*) and Nevada Tiger Beetle (*Ellipsoptera nevadica*) perhaps spread north into southern-most Manitoba during or since the warm-dry period around 6,000 years ago, as part of the mixed-grass prairie biota. During historic times, both species appear to have declined to single small populations, which have subsequently disappeared from the region due to chance or destructive changes in their habitats. The species' main ranges now lie many hundreds of kilometres to the south in North Dakota. With the flighted dispersal abilities of tiger beetles, there is a slight chance that one or both of these species may return someday to some low-impacted sites (i.e., in parks and protected areas).

The astounding innovation of flight in insects is believed to have evolved about 400 million years ago (in the Devonian Period), and heralded an explosion in species diversity and ecosystem exploitation of insects that has remained to this very day. By 300 million years ago (Permian Period), beetles had evolved two special sets of wings – hard protective forewings and delicate, folded, flight hindwings underneath, where they lay protected when not in use. The process of natural selection, operating over this great duration of time, has achieved perfection in wing design and function. Wings are responsible for the great dispersal abilities of tiger beetles, enabling them to find new sites to inhabit. Yager and Spangler (1997) found that Aridland Tiger Beetle (*Ellipsoptera marutha*) could fly strongly on a tether, without any wind stream, and show signs of fatigue only after 30 to 45 minutes of continuous flight. Individuals flew more readily in the morning and evening, and were reluctant to do so in the afternoon. Wings also play crucial roles in the search for food, predator avoidance (escape and camouflage), thermoregulation, and courtship.

CO-EXISTING SPECIES OF TIGER BEETLES

Frequently, more than one species of tiger beetle may be found inhabiting the same site, although there are likely subtle differences in their habitat utilization (i.e., niche partitioning). Typically, the sizes of these species will differ, demonstrating that they are focussing on different types, sizes, and other attributes of prey. Mandibular dimensions and size of teeth also vary considerably among tiger beetles – a reflection of adaptations to handle different size prey (Pearson and Mury 1979). Manitoba's largest species, the 20-mm *Cicindela formosa,* can overpower bigger prey than the 15-mm *Cicindela lengi*, which in turn takes larger prey than the tiny, 10-mm *Ellipsoptera lepida*.



Bargaining Beetles. Okay big fella, let's go over this one last time. You take the big hairy caterpillars, fat grasshopper nymphs, and stinky stink bugs, and leave the little buggers like ants, spiders, and flies for me, right? (cartoon: Rob Gillespie; concept: Robert Wrigley)

Advancing dunes in the Carberry Sandhills, which segregate the tiger beetle species found on sandy trails through arid mixed-grass prairie (e.g., *Cicindela lengi* and *Cicindelidia punctulata*) from those present on barren or partially vegetated dunes (e.g., *Cicindela limbata* and *Ellipsoptera lepida*). Only *Cicindela formosa* and *Cicindela scutellaris* were recorded consistently in both distinctive habitats. (© Robert Wrigley)

The following 11 species of tiger beetles were taken (eight on 9 April 2001, and 16 August 2003) along a sandy prairie trail and adjacent active dunes in the Carberry Sandhills of southwestern Manitoba (in order of abundant to rare):

Cicindela formosa
Cicindela limbata
Cicindela repanda
Cicindela scutellaris
Cicindela lengi
Cicindela tranquebarica
Cicindela duodecimguttata
Ellipsoptera lepida
Cicindelidia punctulata
Cicindela purpurea
Cicindela limbalis

Forestry Road south of Lewis. (© Robert Wrigley)

In a remarkable example of 'species packing,'10 species of tiger beetles were recorded (not all on the same date) along a sandy trail called Lewis Forestry Road (south of Highway 15) through Jack Pine-Poplar Forest and willow-alder thickets in southeastern Manitoba (in order of abundant to rare):

Cicindela longilabris
Cicindela scutellaris
Cicindela formosa
Cicindela tranquebarica
Cicindela repanda
Cicindela purpurea
Cicindela duodecimguttata
Parvindela terricola
Cicindela denikei
Cicindela limbalis

These examples provide evidence of habitat diversity and quality (i.e., least altered by human activities in the former), local species richness, competitive avoidance, and differences in adult seasonality. The Carberry Sandhills are situated at the intersection of the Grassland, Boreal Forest, and Mixed Forest biomes, each contributing their representative biotas, resulting in 14 species of tiger beetles being found there. *Ellipsoptera lepida* and *Cicindelidia punctulata* reach their northern peripheral limits of distribution in these sandhills. The Lewis Forestry Road opened up invasive opportunities for the 10 species of tiger beetles in an otherwise entirely unsuitable habitat of dense Jack Pine forest. Melius (2009) also noted overlapping preferences among eight species of tiger beetles for different microhabitats within and adjacent to salt flats in the Laguna del Perro region of New Mexico. Each species was limited to one or two microhabitats, demonstrating habitat partitioning during the short post-monsoonal period.

OBSERVING TIGER BEETLES

Most people who have hiked a variety of Manitoba trails and other wild places will have come across tiger beetles, but to the casual observer, these just appear as some unidentifiable insect flying ahead or off into nearby vegetation. This was my usual experience as well, until I was introduced up-close to these fascinating insects. Many species are brightly or cryptically coloured and patterned with white dashes and spots (i.e., maculations) on the wing covers (elytra), and consequently appear invisible on the ground, and then vanish after landing on similarly coloured substrates, or into visually complex backgrounds such as vegetation or gravel. Tiger beetles are highly alert, quick to detect one's approach, and fly off rapidly, low over the ground, usually to within 2 to 5 metres. It is therefore important to draw near slowly, keeping a low profile, and without making any sudden movement, which the beetle would be quick to detect and react. In fact tiger beetles seldom fly unless disturbed, preferring to run on the ground, thereby saving energy (Willis 1967).

Although challenging to detect, a beetle first leaps into the air to avoid striking the delicate underwings on the substrate. It then fully opens its folded wings from under the raised wing covers and flies rapidly away. The flight wings extend and beat so rapidly that one cannot see them in operation, and they are withdrawn with equal speed before landing. A buzzing sound is sometimes heard arising from the rapidly vibrating wings, generally a trait of *Cicindela formosa* and other large species. Sometimes landing with a bounce or tumble, the beetle instantly repositions itself to face the observer. This maneuver is repeated a couple of times as the observer continues along the trail, but then the beetle may fly right past the observer to return to its home range, indicative that it perceives its familiar natural surroundings. The several smaller Manitoba species, such as *Ellipsoptera lepida* and *Parvindela terricola*, escape with either short flights, or simply by running rapidly to a perceived safe distance into nearby cover.

A Big Sand Tiger Beetle (*Cicindela formosa*) excavating a temporary burrow in the sand in a shaded site. (© Larry de March)

While tiger beetles disturbed in their natural habitat generally fly from 2 to 5 metres before landing, they are capable of remaining airborne for several kilometres (Stanton and Kurczewski 1999). Presumably this occurs when dispersing to new sites. It has been the author's experience over the years that he has lost sight of over half the number of the beetles he startled into flight. Some people have better eyesight than others in this regard.

Under windy conditions, with gusts sufficiently strong to send sand grains into the air, the author has observed *Cicindela formosa, C. limbata,* and *Ellipsoptera lepida* seek refuge in calm valleys among the dunes, hide under cover of vegetation, or quickly excavate a shallow burrow in which to hide temporarily. It is fascinating to watch a tiger beetle scatter sand grains with its rapidly kicking legs, ultimately disappearing headfirst into the burrow. Individuals struck by a gust of wind may be tumbled over the sand or mud a short distance, then regain their footing and retreat to a sheltered spot. Occasionally a tiger beetle will refuse to take flight even when pursued, and it is likely that the individual is weakened from old age or injury. Tiger beetles often pause during their various activities to groom their bodies, antennae and mouthparts, using rapid sweeping motions of their stiff, setae-covered legs to sweep away dust, sand grains, and remains of masticated prey (Willis 1967, personal observations).

If one searches out suitable habitats within species' ranges, as described in the current accounts, try to spot a tiger beetle while it is undisturbed and stationary by developing a 'search image,' noting their characteristic colour pattern and size. Once chased off its original spot, an alert beetle becomes more difficult to approach closely. With the aid of binoculars, and a slow, low-profile approach, there is a good chance that one can become proficient in identifying the local species, once their characteristics are learned. The customary technique used in studying and identifying a tiger beetle is to capture it in an aerial net, whereupon it may be held gently in the fingers and examined at close range. The beetle may attempt to bite with its impressive mandibles, but they cannot penetrate one's finger, and it usually ejects brown digestive juices as a defensive mechanism. Lacking a net, the author has occasionally captured a beetle by hand, but this is usually an exercise in frustration, as the beetle adeptly evades the hand at the last second. A few arid-grassland species of the American Southwest, such as the White-striped Tiger Beetle (*Parvindela lemniscata*), are highly attracted to ultraviolet or mercury-vapour lights, and the author has experienced instances of literally hundreds of individuals arriving at a light trap after dark, landing on a white sheet and all over his body. However, he has not experienced such numbers of any species in Manitoba.

The amazing-looking tiger beetle larva may sometimes be captured by placing a long, stiff grass stem (frayed or with a bent 'hook' at the end) down into the burrow, and then pulling out the attached larva when it bites and holds onto the stem (i.e., 'jigging'). One may attempt to block the descent of a larva down its burrow with a slicing action of a knife under the sand. Another technique, involving more effort, is to excavate the soil around an inserted stem to reach the inhabitant. In over two decades of searching for tiger beetles, the author has found only one larva (*Cicindela formosa*) out of its burrow. Perhaps its home became uninhabitable for some reason, or a predator or large prey pulled it out. Techniques and equipment for rearing tiger beetles in captivity have been described by several authors (e.g., Shelford 1908; Palmer 1979, Leonard and Bell 1999).

Dawson and Horn (1928) made the following captivating observation. "An interesting demonstration of these larvae and their burrows may often be had where they are common by standing quietly for a few minutes, then suddenly stamping upon the ground, or moving the arm so as to cast a shadow across the bare ground. The sudden dropping of all tiger beetle larvae from the mouths of their burrows seems magically to perforate the ground with numbers of sharply outlined round holes. After a few moments of quiet the holes unobtrusively disappear as they are 'plugged' one after another by the heads of the occupants."

Larvae of Tiger Beetles. The one on the left is likely an Oblique-lined Tiger Beetle (*Cicindela tranquebarica*), a common species in the Sandilands Forest Reserve (east of La Broquerie, Manitoba) observed on 28 July 2020. Note the pair of sharp mandibles, two pairs of black eyes, and the hardened flat plate formed by the head and pronotum, which the larva situates to seal and camouflage the entrance of the burrow. Only 60% of United States and Canadian tiger beetle larvae have been described, and no comprehensive key for identification yet exists. (© Deanna Dodgson)

Suitable sites to search for tiger beetles include the shores of lakes, ponds and rivers, mudflats, sand dunes, sandy blowouts, paths through woodland, prairie and meadows, eroded clay banks, barren spots in salt marshes, smooth outcroppings of rocks, gravel pits, and roadsides with spots devoid of vegetation. The common feature among these diverse habitats is bare or partially bare substrate; that is, devoid of thick plant growth, which affords the beetles open spaces in which to navigate freely, hunt for prey, and to detect the approach of a predator – all of these factors relying on vision. In contrast, and providing a significant example of niche segregation, most members of the related ground beetle family (Carabidae) prefer dense cover or debris in forest, shrub, grassland, and sedge-moss habitats. Ground beetles are mainly nocturnal and have relatively small eyes, offering limited vision, while Manitoba tiger beetles are diurnal (A few species are also active at night) and have prominent eyes.

“The tiger beetle larvae are as ugly and ungraceful as the adults are beautiful. The two have only one habit in common – their eagerness for prey...[The larva’s] rapacious jaws extend upward, wide open, ready to sieze the first unwary insect that walks over this living trap, or near it; for a larva will throw its body forward some distance in order to seize its prey.” (John Henry Comstock, 1940. An Introduction of Entomology)

An example of a temporary habitat (a clay roadway) opened recently in White Spruce-Poplar forest west of Rennie, which provides essential burrow sites and prey (e.g., ants, true bugs, flies) for tiger beetles. Species collected here over the years were *Cicindela limbalis, C. denikei, C. tranquebarica*, *C. longilabris,* and *C. purpurea* (in descending order of abundance). (© Robert Wrigley)

Tiger beetles are excellent subjects to observe in their native habitats as well as in the confines of a terrarium. Witnessing a tiger beetle track down prey, interact with other individuals, attempt copulation, and other fascinating behaviours (all at high speed) provide glimpses of their special adaptations leading to their remarkable success around the globe for millions of years. These beetles have been studied by professional entomologists and amateur enthusiasts for over two centuries, and they will no doubt attract countless others in the future. These insects present an endless variety of questions and avenues to investigate in both the field and laboratory. On our part, we have felt great excitement on so many occasions when travelling along seldom-travelled trails and roads in search of unrecorded sites for tiger beetles. Often these searches prove fruitless, but when one discovers a new population within or outside the currently known range, or observes some unanticipated behavour, like a tiger beetle deftly tracking a bug, the experience is arresting, and makes one's day in the field.

To fully appreciate these beetles' impressive physical attributes, try observing a live specimen with a hand lens, or a preserved specimen under a microscope. The head, with its bulbous eyes, impressive set of toothed mandibles and projecting palps, the wing covers with fine microsculpture (pits, bumps) and brilliant colours, and contrasting patches of white setae, are true marvels of Nature's designs, fully capable of inspiring a movie on aliens from outer space. Although tiger beetle species represent only 0.7% of the province's current beetle list of 2680, they are arguably the most charismatic and easily observed members of our coleopteran fauna. Enjoying the antics of a tiger beetle along a trail may be the highlight of a hike, and presents a wonderful opportunity to interest youths in natural history.

While relatively few individuals go to the effort of collecting and curating specimens of tiger beetles, countless naturalists have taken up the hobby of insect and general-nature photography. Books and internet sites are currently richly illustrated with remarkable photographs of all but the rarest of tiger beetle species, taken by professional and amateur photographers who happened to be fortunate enough to come across an obliging specimen. Approaching a tiger beetle sufficiently close for a good photo may on occasion be exasperating, since these insects have such excellent vision and don't take lightly to close encounters, so they either repeatedly keep running away or take flight out of range, never to be relocated again. A sharp photo, therefore, is a real achievement, and something to be prized.

TIGER BEETLES AS PREDATORS

The two most-important limiting resources for tiger beetles are food and egg-laying sites, since the rate of food intake by the larva affects the size of later instars and the adult, which in turn affects adult fecundity (Pearson 1988). Both larvae and adults are predatory, attacking ants, beetles, bugs, spiders, flies, caterpillars, and other small arthropods that wander within range, and which can be overpowered. Larvae have been reported to capture prey 50 times their own body mass (Brust and Reese 2020), while adults generally capture prey no larger than one-tenth the length of the beetle (Pearson 1988). Willis (1967) provided an extensive list of arthropods observed being attacked and eaten by tiger beetles in the field and laboratory. Dead arthropods are also scavenged. The long, thin legs, small trochanters (second leg segment or 'shoulder'), and associated muscles of the adult tiger beetle enable it to run rapidly after prey, and across various substrates such as lichen-covered rock, loose sand, gravel, and wet mud. The author has collected several specimens with ant heads and jaws firmly attached to the beetle's legs; evidence that the ants were aggressively attempting to defend themselves from predation. Deanna Dodgson informed the author that she observed a *Cicindela formosa* stalking three male, interacting sand wasps (*Bembix pallidipicta*), as they 'hopped' across the sand in the Spruce Woods Provincial Park. Although the beetle made contact with its mandibles on two wasps, it failed to hold onto them.

A *Cicindela purpurea* devouring a lady beetle. (© Larry de March)

A tiger beetle is often seen actively searching for either prey or a mate. An alternative hunting strategy is to sit and wait for prey to approach, and then to ambush it with a series of rapid direct attacks. It then proceeds to grasp and clench the prey repeatedly with its sharp, toothed mandibles. Mandibular length is highly correlated with prey size (Pearson and Mury 1979). A tiger beetle masticates its prey using its mandibles and molars, but is unable to swallow solid pieces of prey; it simply ingests prey fluids using pre-oral digestion. These active hunting techniques of diurnal, flighted tiger beetles are not utilized by the flightless, nocturnal night-stalking tiger beetles (*Omus*) and giant tiger beetles (*Amblycheila*), which are unable to move rapidly. They rely on their antennae for olfaction and to sense prey movement, and nerve cells on their legs to detect prey vibrations through the substrate. Their small, flat eyes (with fewer ommatidia or visual units) appear of little use in finding prey. Interestingly, the nocturnal, metallic-coloured, big-headed tiger beetles (*Tetracha*) have large eyes, rapid running capabilities, and hunting strategies similar to diurnal *Cicindela* species. It seems likely their ancestral line was originally diurnal.

The prominent, bulging eyes in diurnal species, and pair of 11-segmented antennae held in forward position, are the means of locating and tracking down prey. Arthropods are pursued with an unusual form of behaviour involving a number of rapid sprints interspersed with pauses in order to relocate the direction of moving prey – 'pause and look behaviour' – similar to a recalculating navigational device. This adaptation is thought to be due to the beetle moving considerably faster than its visual-neural system can process incoming information. In fact, tiger beetles are suspected of being the fastest-running of all insects. Flightless *Cicindela* (*Rivacicindela*) *hudsoni* of Australia has been recorded running at up to 2.5 metres/second (Kamoun and Hogenhoult 1996). The visual field of the large compound eyes of tiger beetles (each eye consisting of several thousand ommatidia) actually provide binocular overlap (from 40 to 120 degrees), enabling some degree of three-dimensional vision, and along with colour sensitivity, permit the beetle to accurate track its evading prey (Friedrichs 1931). Tiger beetle eyes have adapted to detect the slightest movements of prey, and if the latter stops moving, the beetle is usually unable to identify it, and may swing the antennae forward to make contact. The author has observed beetles momentarily pursuing wind-blown pieces of debris. Over time, tiger beetles learn to recognize the size, escape potential, and likely location of prey, and to apply different tactics, all of which contribute to greater hunting success (Rewicz and Jaskula 2018).

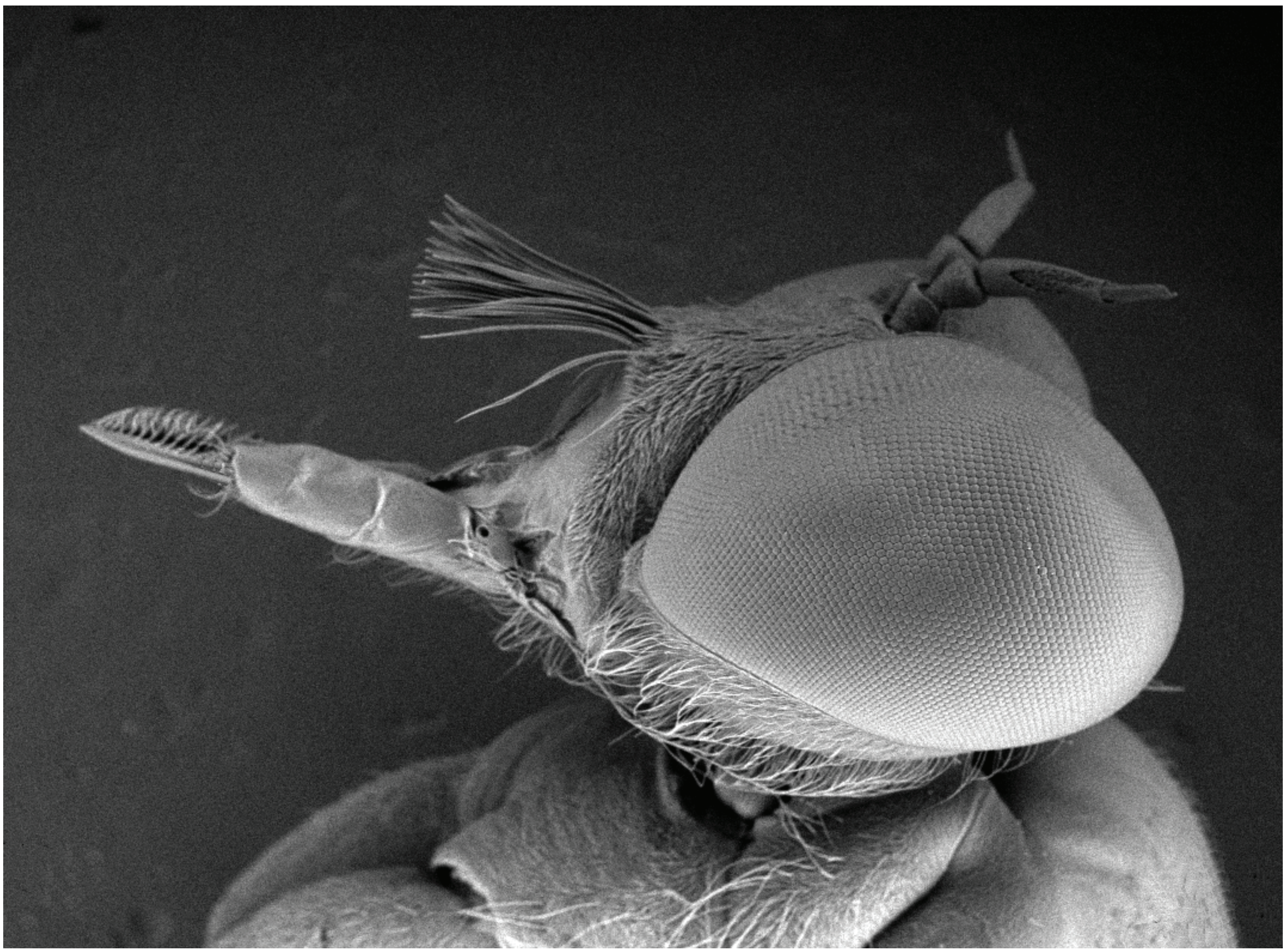
The fiercesome-looking Laurentian Tiger Beetle, well equipped to detect the presence, pursue, seize, masticate, and ingest the fluids of a wide variety of prey. (© Larry de March)

Resh and Carde (2003) state; "The most impressive of all larval ocelli [eyes] are found in tiger beetles (*Cicindela*). These have a lifestyle similar to that of ant lions, ambushing insect prey as they pass their burrows. There are again six ocelli on each side of the head, but two are much larger than the others. The largest has a diameter of 0.2 mm and a retina containing 6350 receptors. The interceptor angle is about 1.8°, comparable with or better than the resolution of compound eyes of most adult insects."

The movements of prey activate neurons in the cicindelid larva's two pairs of large single-lens eyes (stemmata), which releases a rapid, backward body-reflex extension and mandibular grasp onto the prey (Lin and Strausfeld 2013). Acute eyesight, an ability to detect vibrations from prey, and rapid reaction time (i.e., an ambush-hunting lifestyle) are critical abilities of the larva when relying on prey that only occasionally wander within range of the larval burrow. Lack of food means delay of larval growth and moulting, and possible starvation. Interestingly, all the larva's eyes disintegrate during the beetle's metamorphosis in the pupal stage, and one pair of large compound eyes are formed.

TIGER BEETLES AS PREY

Tiger beetles' cryptic pattern of colours and maculations, rapid flight, flash of iridescent colour of the abdomen in sunlight, 'freezing' on landing, and habit of seeking cover are all instrumental in either their escaping the notice of, or pursuit by, predators. Although fleet of foot and in flight, there are predators that manage to catch them, such as robber flies (e.g., *Stenopogon inquinatus*, Asilidae), dragonflies, hister beetles (*Saprinus*), predatory bugs, spiders, frogs, toads, lizards, birds, and mammals such as skunks and raccoons (Graves 1962, Larochelle 1974, Pearson and Vogler 2001). Helzer (2016) photographed a dramatic scene of a large robber fly capturing a *C. limbata* in mid-air. The fly's mouthparts succeeded in separating the beetle's tough elytra and then injected digestive enzymes into the beetle, which ceased activity in a few minutes. Judd (1898) noted that the diet of the Loggerhead Shrike (*Lanius ludovicianus*) and Northern Shrike (*Lanius excubitor*) included a large percentage of insects, with significant numbers of adult tiger beetles, especially in early summer before grasshoppers became abundant, based on data supplied by Ernest Thompson Seton (perhaps when he studied wildlife in the Carberry Sandhills from 1882-1883). Brust and Reese (2020) reported the Northern Flicker (*Colaptes auratus*), shorebirds, and velvet ants (wasps in the family Mutillidae) as significant predators of tiger beetle adults and larvae.



A robber fly's piercing proboscis (hypopharynx) injects a paralyzing saliva (with neurotoxins and proteolytic enzymes) into a tiger beetle, rapidly immobilizing it. The beetle's liquefied internal contents are then sucked up through the proboscis. (SEM © Erwin Huebner).

Acorn (1991) observed *Cicindela formos*a attacking and feeding on *C. limbata* and *Ellipsoptera lepida* in Alberta sandhills. In laboratory trials, Hoback et al. (2008) found that *C. circumpicta* attacked and ate (with a frequency of 38% for males, 50% for females) the smaller species *C. togata*. The large *C. formosa* is likely capable of preying on the other smaller species of tiger beetles found regularly in sandy habitats in Manitoba. The author found a dead *Cicindela scutellaris* in the mandibles of a jumping spider.

This jumping spider (*Phidippus purpuratus* Keyserling) succeeded in capturing a Festive Tiger Beetle – a feat requiring speed of attack and strength to hold onto a struggling prey. The site was a sandy trail through prairie at Mars Hill WMA, where the beetle was common at the time. (© Robert Wrigley)

An adult tiger beetle's main defense from predators lies in avoidance, with reliance on vision and rapid flight (Pearson and Vogler 2001). In addition, a pair of tympanic hearing organs, situated under the elytra, are sensitive to high-frequency sounds, and are suspected to be of value in detecting the presence, and subsequent eluding, of flying predators such as insects and bats. These organs may also be utilized in intraspecific communication (Spangler 1988), arising from stridulary (sound-generating) structures of the elytra and hind tibiae (Freitag and Lee 1972). Willis (1967) remarked on seeing *Cicindela repanda*, *C. fulgida* and *Ellipsoptera nevadica* raising their elytra slightly and making short buzzing sounds.

On a warm afternoon, tiger beetles become highly active and may be impossible to approach closely, and when they take flight, they usually travel repeatedly for many metres, often out of sight. In such circumstances, predators would be challenged to relocate its beetle prey. Certain species that are often abundant (i.e., dozens or more) at a site, for example *Cicindela repanda* on mud flats, alert each other when a predator looms. One can observe that as a single beetle takes flight and lands nearby, many others are stimulated to retreat as well. The sudden flying swarm of numerous beetles scattering in many directions readily distracts a human collector, and quite likely a natural predator. When not actively hunting for a meal or a mate, tiger beetles often remain motionless for many minutes, or conceal themselves under debris, thereby avoiding detection by potential predators.

When attacked by a predator, or handled by a person, an adult tiger beetle applies its impressive mandibles in defense, and expresses digestive juices from adjacent mandibular glands, which likely cause a stinging sensation in the mouth of a predator, perhaps resulting in release of the beetle (Pearson et al. 2015). Certain adult tiger beetles also secrete defensive volatile, burning chemicals (benzaldehyde, hydrogen cyanide, and mandelonitril) from pygidial glands located near the tip of the abdomen, which discourage predation (Moore and Brown 1971, Blum et al. 1981, Pearson and Vogler 2001).

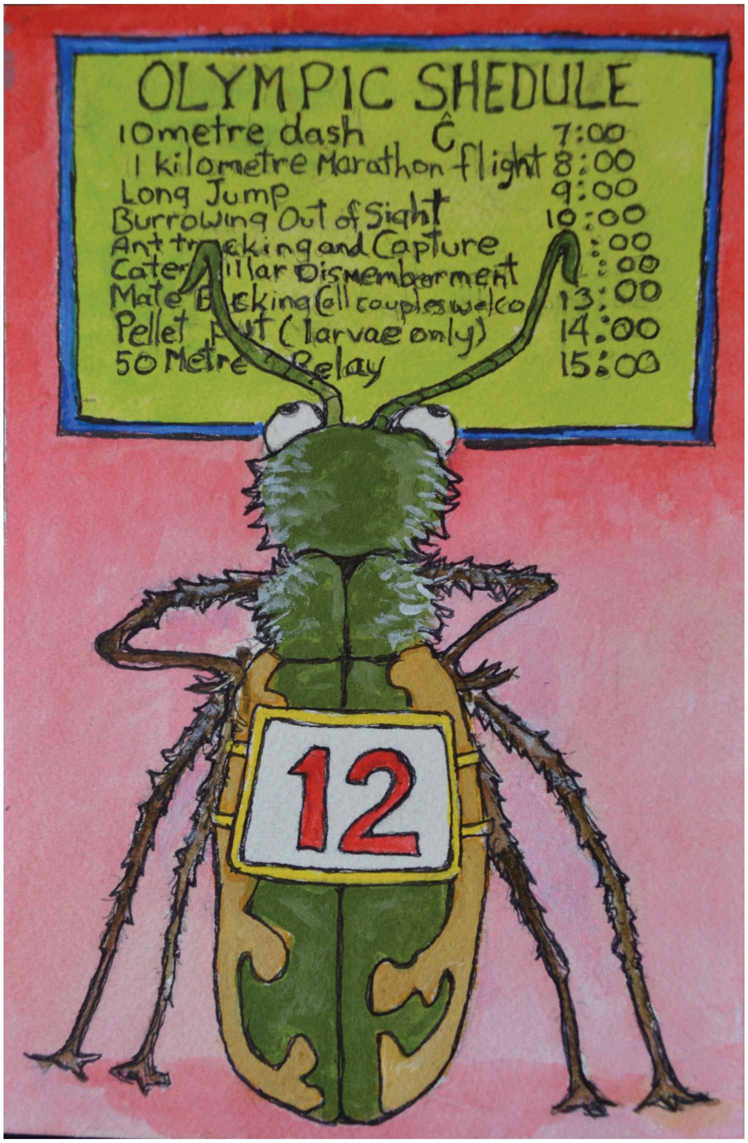
Criddle (1907) stated that: "The beetles [larvae] are sometimes destroyed in large numbers by badgers." Larval tiger beetles are also preyed on by ants, lizards and birds (Pearson 1985). Acorn (2004) stated that flickers [e.g., Northern Flicker, *Colaptes auratus*] are known to capture tiger beetle larvae at the entrance of the burrow with a quick jab of their long bill. Larvae are parasitized by bee-flies (e.g., *Anthrax analis,* Bombyliidae), wasps (*Methocha* and *Pterombrus* species, Tiphiidae), and mites. Mortality rates from these parasitoids have been found to range from 6% to 80% (Pearson and Vogler 2001). A bee-fly deposits an egg at the beetle larva's burrow entrance, where it soon drops to the bottom. When the bee-fly egg hatches, the larva attacks and devours the beetle larva or pupa (Shelford 1908). Thin-bodied, flightless female wasps can enter a tiger beetle larval burrow, where they are usually attacked by the resident, but still manage to sting the larva in the neck, paralyzing it. The wasp then glues an egg to its host, climbs back up the burrow, and seals it with soil before departing. The wasp larva devours the beetle larva and completes its stage of development within three weeks (Pearson 2015; Knisley and Schultz 1997; (https://www.chrysis.net/methocha/Methocha_overview.htm). Wilson and Farish (1973) reported female *Methocha stygia* wasps transporting *Cicindela* larvae to its own nest site.

A tiger beetle larva remains hidden inside its burrow, but can be extracted or dug out by predators, although the depth and curves of the tunnel may frustrate most attempts. Two pairs of spines and stiff bristles on the humped back of the fifth abdominal segment act as grappling hooks, helping to prevent the larva from being pulled from its burrow by both a large prey or a predator, thereby gaining a chance to escape by dropping to the bottom of the burrow. Unlike most other beetle larvae, which have poor vision, the eyes of a larval tiger beetle are packed with photoreceptors which allow for shadow detection and detailed focusing of prey and predators. The larva is also readily alerted by vibrations in the soil, arising from the approach of some large creature (Willis 1967, Pearson and Vogler 2001). Consequently, a person rarely comes across a larva remaining stationed at the top of its burrow. The larva's flat head, almost sealing the entrance to the burrow, also serves to conceal its presence. When pinched in the abdomen, tiger beetle larvae (e.g., *Cicindela lengi*, *C. duodecimguttata*, and *C. tranquebarica*) outside the burrow have been observed to rapidly flex their bodies, resulting in their somersaulting into the air or rolling away for some distance, which is thought to be an escape reaction when attacked by a predator, or when about to be stung by a parasitoid wasp (Harvey and Acorn 2019).

ACTIVITY

Although all Manitoba species are diurnal, *Cicindela limbata, C. repanda, Ellipsoptera lepida, E. nevadica, E. cuprascens,* and *Cicindelidia punctulata* may also be active at night, related to feeding and dispersion (Vaurie 1950, Willis 1967, Pearson et al. 2015, personal observations). Larvae remain ready to attack prey both day and night (Pearson et al. 2015). Over many years, the author has observed numerous *Cicindelidia punctulata* highly active at lights in a dozen states in the USA, but not in Manitoba due to the species' rarity and distance of populations from towns. The best opportunities to observe tiger beetles are on warm sunny days, although intermittent or heavy cloud cover often causes them to remain motionless or to hide. The build up of heat throughout the day may send the beetles under cover of vegetation, or inside a temporary shallow burrow. They seek shelter underground during cold nights, and emerge as the rising air temperature reaches about 14°C. Once the beetles have warmed up from basking in the sun, they become highly active, and are therefore more challenging to approach or capture.

A tiger beetle traverses its home area by creeping, or in start-and-stop fashion, almost always in 'high gear.' A significant part of each day is also spent in bouts of sweeping its head, thorax and abdomen clear of sand and dust particles with rapid, sweeping strokes of a leg, using all six legs (one leg at a time) to reach all areas of the body. As if to ensure its mandibles are clean and ready for action, the beetle frequently clenches and spreads open these mouth parts.



With their remarkable physical attributes and complex behaviours, tiger beetles would excel in active competition with other kinds of insects. (cartoon: Rob Gillespie; concept: Robert Wrigley)

Willis (1967) concluded that; "The primary factors that govern the activity of adults seem to be temperature, humidity (actually evaporation), probably light, and wind." Gusts of wind may send tiger beetles tumbling, until they can regain their feet. On a day with high winds in the Carberry Sandhills, the author observed several *Cicindela formosa* rapidly excavate temporary retreats in the sand. Digging alternatively with first the front legs, and then kicking the sand backwards with opposite thrusts of the hind legs, the beetle disappeared within two minutes. Nearby he spotted a *Cicindela limbata* with only its rear end sticking out of its short burrow. With limited beetle activity on the dune surface, it was apparent that the beetles preferred to avoid the powerful gusts – sufficiently strong to cause drifting sand, and to sting the author's bare legs.

Like other mobile insects, tiger beetles thermoregulate through a variety of behaviours, such as basking on dark substrates, and shuttling back and forth to shade. In fact, they may direct over half their daily activity to maintaining a high internal body temperature, which remarkably may reach as high as 39°C, just below their lethal limit (Pearson et al. 2015). Such elevated temperatures promote the beetle's high speed, both running and flying, which are crucial in capturing prey and escaping predators. The author has observed several species of tiger beetles (e.g., *Cicindela formosa*) land on and bask atop pocket gopher mounds. These elevated, dark, unvegetated sites offer a slightly higher temperature on cool mornings, as well as excellent sight lines in detecting the movements of passing prey. An early-spring species, such as *Cicindela purpurea*, would likely be able to become mobile at a lower temperature than a summer-active species such as *Ellipsoptera lepida.*

Pearson and Lederhouse (1987) measured thoracic temperatures in 13 desert-dwelling species of the tribe Cicindelini near Willcox, Arizona, and found coordinated-walking minimal temperatures at 14-21°C, basking behaviour at 29-33°C, foraging at 30-37°C, and stilting and shuttling to shade (to prevent overheating) at 37-39°C. Chapman et al. (1926), in a study of sand dune insects in Minnesota, found that *Ellipsoptera lepida* and *Cicindela formosa* became active at 15-20°C, with the former dying at 45-50°C and the latter at 50-55°C. Morgan (1985) demonstrated basking behaviour in *Cicindela tranquebarica* to maintain a body temperature between 33 and 38°C. Both time spent seaching and searching speed were positively correlated with body temperature, thereby improving the beetle's probability of finding more prey and mates.

During inclement weather and overnight, the beetles remain in burrows or seek cover under stones and other debris, quickly emerging if the sun appears and warms the substrate to over 14°C (personal observations). As the day warms up, individuals may be seen to rise high on their long legs (stilting), lifting the body as far as possible above the hot substrate, and/or to position the body at an incline facing the sun, thereby reducing its exposed profile. Acorn (1992) believed that the dark areas of the elytra (wing covers) are important in thermoregulation, through the absorption of infrared radiation. The Ghost Tiger Beetle (*Ellipsoptera lepida*) and Sandy Tiger Beetle (*Cicindela limbata nympha*) are mainly white (with sparse, light-brown or -bronze maculations), which reflects solar rays and helps prevent overheating in their exposed habitats. The underside of the body in most species is a shiny green, blue or purple mirror, which likely reflects away some substrate heat. Numerous white hairs (setae) on the legs, underparts, and dense patches of white setae and bristles on the head and prothorax, likely also help in thermoregulation through insulation and by reflecting away solar radiation, in addition to providing for sensory reception (touch). Appearing in precise patterns and locations, setae are useful in species identification and classification.

On extremely hot afternoons, the beetles rapidly excavate temporary burrows in the cooler soil, seek shade under vegetation or a boulder, or rest on wet mudflats where evaporation cools the surroundings (Pearson and Vogler 2001). The author was able to capture a number of adult *Ellipsoptera lepida* on a hot mid-afternoon by scooping them out of their shallow (about 2-cm) burrows in the sand with a cupped hand. Temporary burrows seldom descend for more than 15 cm, and the beetles are quick to emerge as temperatures become more conducive (Criddle 2015). If conditions continue to deteriorate (e.g., seasonal cold or heat, aridity), larval and adult beetles remain in a deep burrow, or seek some other protected site, and enter diapause during which their metabolism slows, and they remain in this state of suspended animation until conditions improve. Temperature and possibly day-length changes provide cues to approach such a physiological state, which conditions them to survive lengthy climatic extremes. Since Manitoba experiences frozen ground in winter (for at least five months) to a depth of 183 to 240 cm, most overwintering larvae and adults are able to withstand some degree of freezing. Warming soil temperatures in the spring stimulate the synchronized emergence of adults, which ensures the best opportunities for courting and mating.

While certain species of tiger beetles are found in exceptionally arid habitats, many others thrive along the edges of waterbodies, streams, and low-lying areas, so these are productive sites to look for certain species. However, these areas may be subjected to flooding during heavy rainfall, snow melt, and storm surge, and consequently one might expect adaptive behaviours and physiological attributes to permit the beetles' continued or periodic existence in such locations. Mobile adults may fly off to nearby elevated places, and return when their habitat dries out, but larvae, even if they attempt to crawl away, are limited in how far they can move, and are exposed to predation while out of the burrow. Surprisingly, larvae of *Cicindela purpurea* are known to have survived submergence and anoxia in their burrows for up to three weeks (Pearson et al. 2015), and adult neotropical species, such as *Tetracha sobrina*, have survived underwater in a laboratory experiment for 30 hours (Adis 1982). *Phaeoxantha* larvae (species living on Amazonian sandy floodplains) have recovered from being underwater in their tunnels for three months. Preliminary studies have found that the larvae are able to access some oxygen trapped in the burrow and on their bodies, and can also reduce their metabolic rate (and hence need for oxygen, and delay carbon dioxide accumulation) by up to 90% (Zerm et al. 2004).

This photo of the Assiniboine River in the Carberry Sandhills reveals the presence of vegetation close to the water's edge on upper and lower banks. (© Robert Wrigley)

A few years later, a massive flooding event scoured the banks and part of the riparian forest, leaving barren banks and extensive exposed sandbars once the waters receded. Countless tiger beetles (particularly larvae) were washed away, but the newly exposed sandbar habitats were rapidly reoccupied by *Cicindela repanda*. (© Larry de March)

Extended flooding, swift current, and wave action along Manitoba waterways must destroy incredible numbers of tiger beetle larvae, which are likely replaced by nearby breeding adults the following one or two summers (Knisley and Schultz 1997, Zerm and Adis 2001). Criddle (1907) stated; "In fact, it is by no means an uncommon occurrence to find dead specimens of the previous year when digging out live ones. Hundreds were found hibernating in 1906 only five feet above low-water mark in the banks of the Assiniboine River, which the rise of the water in the spring would almost surely totally destroy." Wallis (1967) concluded that some species of tiger beetles were not adversely affected by high concentrations of salts in saline habitats. Apparently the thick exoskeleton of adults and the long spines and setae of larvae and pupae serve as mechanical protection from sharp-edged crystals.

LIFE HISTORY

The life cycles of Manitoba tiger beetles may be separated into two distinct categories regarding their developmental and adult activity periods. Spring-fall species overwinter as larvae and adults, always requiring at least two years in the larval stage. The fresh adults emerge and feed in the autumn, excavate a burrow, and hibernate for the winter. These mate and females lay eggs in the spring, and then die off in the summer. Summer species overwinter twice as larvae, then pupate and emerge as an adult in mid-summer. These then feed, reproduce, and die by late summer or early autumn. Depending on the species, and influenced by prey abundance, the life cycle may take from two to four years to complete, spent mainly in larval stages. Southern populations of a species may require only two years to complete its life cycle, while northern ones need three or four, due to the latter's extended period of dormancy each winter (Pearson and Vogler 2001). The alteration of spring-fall and summer species helps reduce competition for prey and habitat sites.

Female tiger beetles are often larger than males, and the latter are identified by having several segments of the front tarsi dilated and densely pubescent on the underside, which are thought to assist in the male's stability during copulation. The male is often keen to investigate and to try to mount another passing individual of the same, and sometimes of another, species, and even another male. If it is a conspecific female, he attempts to jump on her back, quickly applying his mandibles into the side grooves (i.e., coupling sulci) between the female's prothorax and elytra, and securing his position by placing his front and perhaps also his middle legs around her body, or onto the substrate. She is often capable of resisting his efforts – running, rolling over, and throwing him off – after which a chase usually ensues. The strongest males would tend to be more successful in remaining attached for successful copulation. This requires insertion of the male's aedeagus for a relatively long time, up to an hour for some species (i.e., prolonged amplexus), and after withdrawing, the male usually continues to maintain his position (with the hind and sometimes the middle legs standing on the substrate) for another 2 to 10 minutes, thereby guarding against advances of a male competitor (Pearson and Vogler 2001).

The author has observed numerous instances where males of several species (e.g., *Cicindela formosa*) were reluctant to disengage from their partners until approached to within a metre, whereupon they first try running away while still attached, and then finally disengage before flying off to a perceived safe distance. The instinctual drive to mate is strong in tiger beetles, and they spend significant time and energy in searching for suitable mates, and in multiple coupling attempts.

Mating pair of Sandy Tiger Beetles (*Cicindela limbata*). Note the male's mandibles firm grasp behind the female's thorax, and wide stabilizing stance of the male. (© Larry de March)

Following successful mating, a female tiger beetle searches for, and tests out with her ovipositor, sandy or clay soil in which to oviposit – substrates that will offer minimal resistance to burrow excavation by the larvae. Females of each species demonstrate preferences when selecting burrow sites, with apparent factors being local food availability, soil type and chemistry, moisture, temperature, slope, exposure, and presence of surrounding vegetation. The Laurentian Tiger Beetle (*Cicindela denikei*) spends much of its life on exposed bedrock surfaces, so females must find oviposition sites in nearby soil deposits, often where burrows descend to only to 10-20 cm, and sometimes situated under a flat rock. The female Claybank Tiger Beetle (*Cicindela limbalis*) lays its eggs on a well-drained, often-steep slope of clay soil. The amount of food devoured by a adult female relates directly to the number of eggs she can produce (Pearson et al. 2015).

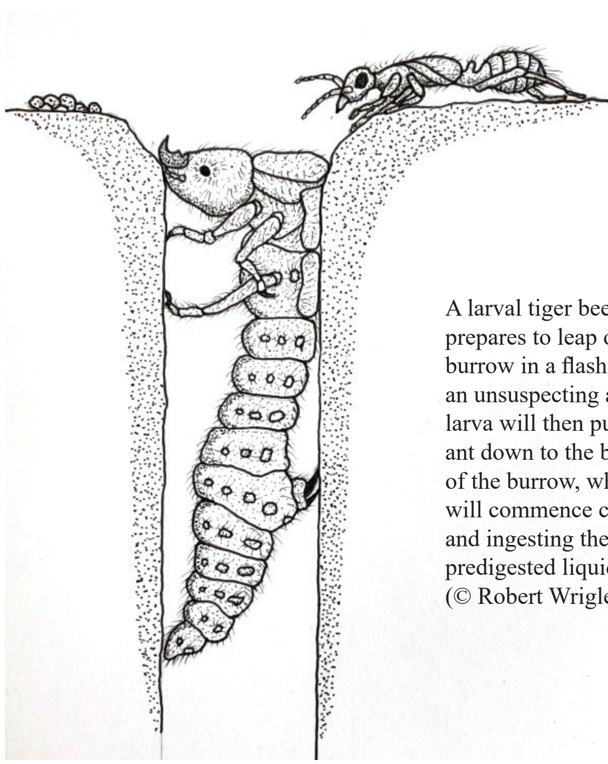
Once a suitable site is discovered, over the next few days the female deposits singly about 50 eggs (each about 2 mm long) from a few to 60 mm into the soil (Shelford 1908, Brust and Reese 2020). The females of most species (e.g., *Cicindela limbalis*) dig into the surface with their ovipositor, while a few others (e.g., *Cicindela formosa*) tunnel into the sand and lay the egg on the side of the burrow, perhaps an adaptation against the egg drying out. The larvae are cannibalistic, so laying eggs at some distance apart likely promotes larval survival (Brust and Reese 2020). However, sometimes numerous burrows are present close to each other. Depending on the species and environment, the egg hatches from 9-38 days (usually around two weeks) after oviposition (Willis 1967, Knisley and Schultz 1997). The white larva enlarges the chamber and then digs downward, using its mandibles to loosen the soil, and its flattened head and thorax to repeatedly shovel the debris out onto the surface. With variations based on the substrate, the entrance may be level on the surface of hard ground or clay, or raised chimney-like around the entrance, or located at the bottom of a funnel in loose sand, into which prey creatures tumble. The larva undergoes three developmental stages (instars), growing in length from about 3 to 13 mm before pupating at the bottom of the burrow (Brust and Reese 2020). The first instar larva needs only one full meal to store sufficient nutrients and calories to moult, while second and third instar larvae require several meals. A larva will accept food every couple of days, but can survive without a meal for weeks. The burrow entrance is closed during feeding, moulting, and pupation (Willis 1967).

Get serious! Am I going to have to lay here frozen in the dark for another winter, just because mother failed to lay my egg in a site with enough prey? (cartoon: Rob Gillespie; concept: Robert Wrigley)

An interesting situation arises in abundant species, such as frequently occurs with *Cicindela repanda*, in regards to potential competition for prey between larvae and adults living in close quarters in the same habitat. Wilson (1978) observed that adults rejected certain prey commonly trapped and devoured by conspecific larvae, thereby minimizing competition, an innate behaviour he described as "prudent predation." However, other entomologists (e.g., Acorn 2001) have doubted the validity of this hypothesis.

The author has seen instances where numerous larvae and adults were located in close proximation. For example, he observed countless *Cicindela repanda* larval burrows and active adults at the steep edge of a sand dune, within two metres of the Assiniboine River in the Carberry Sandhills. Tiny flies gathered on the damp sand appeared to be the main food source. Pearson and Vogler (2001) stated that under such crowded conditions, competition for prey is a limiting factor in larval development and survival, although as noted, larvae can live for weeks without food. Low food availability was found by Mury Meyer (1987) to result in up to 75% mortality in some species. In studying resource use in *Cicindela tranquebarica* and *Cicindelidia punctulata*, she found that a larva's acceptable prey-size range increased with each successive instar, resulting in large (i.e., third instar) larvae having a competitive advantage over smaller conspecifics under conditions of food limitation.

Tiger beetle larvae feed on ants, beetles, spiders, flies, caterpillars, grasshopper nymphs, and other small arthropods that wander within range and that can be overpowered. A larva sits vertically in the burrow entrance with its heavily sclerotized, camouflaged head and prothorax forming a tight lid on the rounded entrance; likened to a manhole cover by Brust and Reese (2020). A thin layer of soil may also accumulate on top of this 'lid', thereby concealing the larva even further (Willis 1967). Following a rain, any soil washed into the burrow is soon tossed out as pellets. When the larva senses the approach of a prey item by sight or vibrations, it leaps out, usually backwards, to half its body length with lightning speed. Clutching the victim with its impressive mandibles, the larva pulls its prey back into the borrow entrance and drops down to the bottom. Both larva and adult dispatch their prey with repeated contractions of their sharp mandibles. A pre-oral mill continues mastication, and the pulpy bolus becomes saturated with digestive enzymes from the mandibular glands. Fluids squeezed from the remains are then pumped into the crop and midgut, and the hard remains are rejected. Tiger beetles can only digest prey liquids (Criddle 1910, Wallis 1967, Pearson and Vogler 2001).



A larval tiger beetle prepares to leap out of its burrow in a flash to grasp an unsuspecting ant. The larva will then pull the ant down to the bottom of the burrow, where it will commence chewing and ingesting the ant's predigested liquids.. (© Robert Wrigley)

As the larva continues feeding, it grows larger after each moult, and continues to deepen the burrow by gnawing, ejecting and packing the soil with its substantial mandibles (Shelford 1908). The third instar larva then plugs the burrow entrance and either drops to the bottom of the burrow, or remains close to the surface in a side pocket, where it transforms into the pupal stage, which lasts for three or more weeks (Pearson and Vogler 2001; https://entomology.unl.edu/tigerbeetle/tiger_biology.htm). The author has rarely found a third-instar larva on the surface; perhaps in these instances the burrow became unsuitable for some reason. The burrow offers concealment from a host of predators and inclement weather conditions. It can often be distinguished from other arthropod burrows by its smooth sides and the soil around the entrance tamped down, although after a rain, there may be discarded pellets surrounding or on one side of the entrance. It resembles a spider burrow, except for lacking the spider's silk coating (Leonard and Bell 1999).
At the appropriate warm season, the newly formed adult (imago) rests inside its burrow for several days, allowing time for its exoskeleton to harden, and then emerges onto the surface where it commences searching for prey and for mating opportunities. Shelford (1917) described in great detail the changes in colour, morphology, and activity of the newly emerged adult tiger beetle. As examples, the new adult can stand and support its weight in 40 hours, begins to dig its way out of the burrow in three days, and commences to hunt and feed in four to seven days.

Regarding phenomena related to senescence of beetles, Crowson (1981) stated; "Old beetles in a population can generally be recognized externally by obvious abrasion of cuticular vestiture, exceptionally dark pigmentation of certain sclerites, and sometimes by loss of apical segments of one or more of the tarsi or antennae." The author has frequently come across aged tiger beetles with atypical patches of dark-brown pigment (common in *Cicindela formosa* in Manitoba sandhills), presumably due to extra deposition of melanin within the cuticular layers of the exoskeleton. Shelford (1917) and Willis (1967) commented on the change in colour of the integument with age, the latter using as example *Cicindela fulgida* being bright red on emergence from the pupal stage, and gradually darkening until death. On August 2, the author found a dead Ghost Tiger Beetle (*Ellipsoptera lepida*) inside a shallow burrow with its entire tarsi worn off from running on abrasive sand. Age may also be estimated by the degree of wear on the tips of the mandibles.

Tiger beetles (in either larval or adult stage) are stimulated into entering winter diapause by the decreasing photoperiod of autumn. They spend about half a year at the bottom of their burrow, which may be 15 cm deep in the Bronzed Tiger Beetle (*Cicindela repanda*) to over 200 cm in the large Big Sand Tiger Beetle (*Cicindela formosa*) (Criddle 1910, Wallis 1961). Surprisingly, Criddle (1907) found occasions when *C. repanda*, *C. duodecimguttata,* and *C. tranquebarica* were found hibernating in the same burrow. Pearson and Vogler (2001) speculated that a set period determines the length of diapause, correlated with the increasing temperature and moisture of the burrow in spring. Synchronization of emergence is important to optimize mating success for individuals and for the reproductive maintenance the population. Most species of adult tiger beetles are active for no more than 8 to 10 weeks, and less for some summer species such as *Ellipsoptera lepida*, and as little as 10-14 days for desert dwelling *Cylindera debilis* (Pearson and Vogler 2001). In Manitoba, rare individuals of some species may be active for up to 20 weeks following early spring emergence.

CONSERVATION

Many species and subspecies of tiger beetles have suffered severe declines in North America and elsewhere due to habitat destruction, the result of intensive cultivation of crops and cattle grazing, water diversion and irrigation, soil erosion, pollution, urban and cottage development, infrastructure such as dams and roads, and recreational activities including all-terrain vehicles and beach foot traffic. Plant succession, flooding, drought, global warming, and other factors pose additional challenges (Knisley and Haines 2007). Canada's Species at Risk (SARA) program, the United States Endangered Species Act, and European Red Lists review the status of tiger beetle species and 'conservation units,' which may justify research, listing, and restorative actions (Vogler and Desalle 1994). SARA lists two endangered species in Canada – the Cobblestone Tiger Beetle (*Cicindelidia marginipennis* DeJean) in New Brunswick, and the Northern Barrens Tiger Beetle (*Cicindela patruela* DeJean) in Ontario and Quebec. A subspecies of the Dark Saltflat Tiger Beetle (*Cicindela parowana wallisi* Calder) in southcentral British Columbia is endangered (Langor 2019), and the subspecies *Cicindela formosa gibsoni* is threatened in the Great Sandhills of southern Saskatchewan and adjacent Alberta (Bell et al. 2019).

However, status recommendation, review, research, approval, and remediation programs are slow processes, and few other tiger beetle taxa have been officially listed to date. Pearson et al. (2015) estimated that 36 (15%) of species and subspecies in the United States and Canada are now so rare and declining that they should be considered for inclusion on the U.S. Fish and Wildlife Service's List of Endangered and Threatened Species, including a number that occur in Manitoba. However, only four are officially listed. Knisley et al. (2014) presented a thorough analysis (with species photographs) of the conservation status of tiger beetles in the United States, and concluded that three taxa were believed to be already extinct, and 62 others were sufficiently rare that they should be listed as threatened or endangered. For example, the Manitoba species, *Ellipsoptera lepida,* has been variously rated as vulnerable, threatened, imperiled, critically endangered, or extirpated in over a dozen states and provinces (https://explorer.natureserve.org/servlet/NatureServe), and yet it is not on the Canadian SARA/COSEWIC, or the U.S. Fish and Wildlife Service's lists.

Many species of tiger beetles are dependent on open habitats, at least partially free of vegetation. With plant succession, populations of tiger beetles cannot fulfill their life cycles and they die out. To combat this loss, wildlife managers (often with the aid of volunteers) have attempted, with some success, to reverse the invasion of plant growth by means of controlled burns, hand cutting, spraying herbicides, grazing with cattle and horses, and hydrological restoration. However these applications must usually be repeated for long-term success (Knisley and Gwiazdowski 2020).

With their specific habitat requirements, sensitively to environmental change, and ease of observation and identification, tiger beetles are an excellent indicator group for evaluating habitat quality and deterioration. Students and citizen scientists are able to contribute valuable information on species' presence and numbers. Pearson et al. (2015) stated in the summary of their classic book on tiger beetles; "Workers can also help in the conservation of these and many other species by noting new information on distribution, population declines, and ecological and habitat limitations of adults and larvae. This information should be published or made available to appropriate workers, [and] land managers of government agencies."

The author has submitted reports to Manitoba Conservation (Wrigley et al. 2008) and the Nature Conservancy of Canada (Manitoba Region) summarizing distributional and ecological findings on tiger beetles and other biota, and in particular, pointed out recommendations for conservation actions. He has also contributed detailed accounts on habitat and conservation-status recommendations for Manitoba tiger beetles to the Manitoba Conservation Data Centre, which serves as a storehouse for information on the province's biodiversity. The Manitoba CDC has a tentative list of species rankings, but it is in need of revision; the author's recommendations are presented in the species accounts. Until Manitoba has an approved official listing of status for all local species of tiger beetles, the following species are recommended for prompt review: *Cicindela hirticollis*, *Cicindela denikei*, *Ellipsoptera lepida*, *E. cuprascens*, and *E. nevadica*. The latter two species were rare and local when first reported in the province, and are likely extirpated, not having been recorded here for over 50 years.

Two things are certain – the conservation status and distributions of Manitoba tiger beetles will continually be altered (usually negatively), with human landscape and habitat appropriation and climate change the main malefactors. The present book serves to document the biology of the 19 native provincial cicindelid species during the early decades of the 21st century. The last two centuries were witness to severe loss and degradation of mixed- and tall-grass prairie ecosystems in southern Manitoba, where most of our tiger species have thrived for thousands of years. It will require the concerted joint efforts by ecologists, wildlife managers and law-makers to ensure that Manitoba's tiger beetles and biodiversity in general do not suffer further losses.

AN APPRECIATION FOR TIGER BEETLES

The author feels a deep sense of appreciation for these exquisite insects, with their beautiful colours, remarkable adaptations, and fascinating behaviours. For over a quarter century, they have drawn me on countless field trips to many of the most-intriguing and wondrous habitats across Canada and the United States. The intense enjoyment felt in the great outdoors in quest of certain species during sunny days and moonless nights is difficult to put into words. These experiences and findings are dutifully recorded in my articles and books, field notebooks, and by the thousands of tiger beetle specimens tagged with my name and data, which will lie for centuries to come in the research collections and exhibits of a number of major museums. The challenging pursuit of these insects has fulfilled in me a remnant of our species' hunter-gatherer instinct, which has largely been quelled by modern life. I feel so fortunate to have been introduced to these beguiling little creatures.

Over the decades, these sentiments about endearing relationships with tiger beetles have been expressed by many other naturalists, two of which I quote below.

"This book summarizes what I have been able to learn about Canadian tiger beetles in a lifetime of which only the leisure hours have been devoted to the study of natural history. Many happy hours have been spent with these insects, both in the field and in my home, and I hope this volume will make it possible for others to share the pleasure that the study of tiger beetles have given to me. (JB Wallis 1961, The Cicindelidae of Canada)

"The quest for tiger beetles leads one to explore far and near. The incentive to wander over the sand dunes, through pine barrens, sunny woods, and along streams, down gravelly shores of rivers and sandy beaches; to go through the heat and discomfort of dry desert wastes, or the quicksand rivers of Arkansas in quest of this or that long-desired species, offers a pleasure that can only be appreciated by the enthusiast who proudly exhibits case after case of his 'tigers'." (Carlos de Wendler-Funaro 1969)

SPECIES ACCOUNTS

(© Larry de March)

Laurentian Tiger Beetle (*Cicindela denikei* Brown, 1934)

Description: This is a bright-green species, immaculate, or with a few small white markings along the outer edges of the elytra. The upper parts of the beetle are covered in minute pits (punctations). It averages slightly larger (13-15 mm) and is more robust than its close relative *C. sexguttata* (10-14 mm) (Kaulbars and Freitag 1993). A blue colour may be seen in a fresh specimen when viewed at a certain angle, and becomes more obvious in preserved specimens.

Similar Species: *Cicindela purpurea* and *C. limbalis* are dull green or reddish and feature prominent white maculations.

Distribution: This species has a limited range from extreme southeastern Manitoba, and adjacent parts of northwestern Ontario and northern Minnesota (Pearson et al. 2015). Remarkably, Bouchard et al. (2005) reported a disjunct population of *C. denikei* on alvars on Manitoulin Island in Lake Superior, but none observed on the adjacent mainland. This *C. denikei* record extends the known range far to the east. Dr. Terry Galloway informed the author that he observed a live specimen on a Winnipeg street, about 100 km west of the species' range. This individual's flight was likely aided by wind, or perhaps it arrived attached to the grill of a car; the author has seen a number of live individuals sitting on a highway with frequent traffic (leading to Winnipeg), as well as road-killed specimens.

Habitat: Wallis (1961) stated that *C. denikei* frequents the summit of rocky knolls among stands of conifers in Manitoba. Kaulbars and Freitag (1993) noted that this is a species of the boreal forest on sandy, silty till, and occurring only on the Canadian Shield. These habitat descriptions are in accordance with the author's many observations – exposed rocky outcrops surrounded by white spruce-jack pine-poplar forest, and also on sandy or gravelly trails, damp sandy soil near rivulets crossing dirt roads, gravel pits, and even primitive parking lots. A paved road is not unlike barren Precambrian Shield bedrock, and the author has captured dozens of specimens along the abandoned (cracked and invaded by early successional vegetation) paved road running parallel to Highway 44, northwest of Rennie. Colonies of ants along the road edges no doubt also featured in attracting the beetles to this unusual habitat.

Activity Period: This is a summer species, with adults active from May to August, but it is most common in June and July. The life cycle likely requires three to four years (Brust and Reese 2020), spent mostly as larvae, and with the adults living up to eight weeks. The adult possibly emerges from the pupal stage in the autumn, then hibernates and emerges in the spring. Larval burrows have been located under flat stones, and the author has discovered both live and dead adults in such locations. Burrows have been reported descending from 10-20 cm (Pearson et al. 2015).

Remarks: This species was named after William Nelson Denike, a Manitoba school principal and entomologist (1871-1948), who collected specimens at Ingolf, Ontario, near the Manitoba border. *C. denikei* was first thought to represent a disjunct, western subspecies of *C. sexguttata* (Wallis 1961), which it closely resembles, even to the point of some individuals of the latter species having reduced spots or absent altogether. However, the distinctive habitat and separate range of *C. denikei* have led researchers to consider it a separate species from *C. sexguttata*. Kaulbars and Freitag (1993) regarded it as a cryptic, sibling species of *C. sexguttata*, the two likely diverging during Late Pleistocene glacial periods.

Populations of the Laurentian Tiger Beetle may vary greatly from year to year, but are usually uncommon. The author has found it relatively abundant on only a few occasions; he observed over 100 individuals on 28 May 2000 within a hectare of prime rocky-outcrop habitat in Manitoba, while in other years only a few or none were seen at the same site. In northwestern Ontario, Brust (2007) found *C. denikei* to be abundant, and watched an adult foraging on an electrical pole about two meters above the ground, and another foraging on the trunk of a standing dead jack pine. He observed that the behaviour of *C. denikei* was quite unique compared to other woodland and boreal tiger beetle species in eastern North America. Adults were typically found actively foraging on open, stony tracks of a gas pipeline, especially in the morning hours, but often flew into the surrounding weedy vegetation when alarmed. Once temperatures exceeded approximately 80° F (26.7° C), adults largely vanished from the trails, and those that were seen typically moved from one location, shaded by plants along the edges of the trail, to another when foraging. Under these conditions, most adults were noted singly on rock outcrops forming openings in the boreal forest. There they actively foraged on the rocky surfaces, never exhibiting the sit and wait ambush behaviour typical of *Cicindela sexguttata.*

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Vulnerable. Recommendation: Vulnerable.

Some level of protection is conferred to the Manitoba population by being located in the Whiteshell Provincial Park. This species was listed as Threatened in Minnesota in 1996 due to its limited range, but with 50 additional populations located recently, it has been changed to Special Concern (Ronald Huber, personal communication). The Ontario Natural Heritage Information Centre (Colin Jones, personal communication) (https://www.ontario.ca/page/natural-heritage-information-centre) and Nature Serve Explorer also list it as Vulnerable.

The Laurentian Tiger Beetle (*Cicindela denikei*) occurs mainly on exposed outcrops of Precambrian Shield in southeastern Manitoba. The bedrock is partially covered with mosses, lichens, and low-growing herbs and shrubs. The beetle does not enter the surrounding forest of Jack Pine, White Spruce and Aspen Poplar. If disturbed, it will fly some distance to reach an adjacent exposed outcrop. This beautiful species looks like a shiny-green emerald while sitting on the gray and pink granite. (© Robert Wrigley)

(© Larry de March)

Twelve-spotted Tiger Beetle (*Cicindela duodecimguttata* Dejean, 1825)

Description: This is a medium-sized (12-15 mm), dark-brown species with metallic blue-green undersides. Maculations are incomplete, the resulting number of dots and bands customarily totalling 12 (leading to the species' latin name). The elytra are bowed out and therefore relatively wide. In southern Manitoba, maculations are often heavy and specimens superficially resemble *C. repanda*; Casey (1913) named this form *"bucolica,"* with Aweme, Manitoba, the type locality. With increasing latitude, maculations become reduced (Wallis 1961). The author has noticed that dark individuals with reduced white maculations are challenging to spot before taking flight, and no easier to detect on landing; with their camouflaged colour, the beetles seem to vanish on dark, wet soils, and among pieces of debris or gravel.

Similar Species: *Cicindela duodecimguttata* is very similar to *C. repanda,* but is generally darker, with no contiguous maculations on the outer elytra, the elytra are more flattened and wider, and the prothorax is relatively wider (Graves and Brzoska 1991, Acorn 2001). The shoulder mark and middle band on the elytral edge are also more widely separated than in *C. repanda*. Some intermediate specimens are difficult to determine. *C. hirticollis* is readily distinguished by the 'G' shape of the shoulder maculation and the tufts of white setae on either side of the thorax.

Distribution: This species ranges across the southern two-thirds of the province, with populations present in almost any suitable habitat. Lawton (2018) extended the range 330 km north to the Nelson River, Manitoba. Remarkably widespread, it occurs east of the Rocky Mountains from the southern Northwest Territories and Alberta to Labrador and Newfoundland, and south to Texas and Georgia. Rather surprisingly, for a species exhibiting such an expansive distribution, no subspecies have been described.

Habitat: This is a common species along riverbanks and ponds, wherever there is exposed wet mud, sand, or fine gravel. Criddle (1907) reported that it prefers localities close to running streams, often going right to the water's edge in search of food. It can also be found alongside watering holes in grazing land, sloughs, roadside ditches, and salt flats. When in association with *C. repanda*, *C. duodecimguttata* tends to move away from the water's edge to drier sites, reducing habitat overlap (Hilchie 1985). It is found more frequently on darker, gravely substrate, while its more-common relative, *C. repanda*, occurs on sandy substrate (Dunn 1981, Graves 1965). In the Athabasca Sand Dunes of Saskatchewan, Acorn (1994) observed this species throughout the dune field as well as on the beach, and considered it more abundant here than on southern inland dune fields. Willis (1967) reported it from fluvial mesic and saline habitats. The author found this species considerably less common than *C. repanda.*

Activity Period: This is a spring-fall species with a life cycle of two years (Dunn 1981, Knisley and Schultz 1997). Larvae overwinter the first year, adults emerge in late summer and fall, hibernate over the winter, and are active again and mate the following spring (Hilchie 1985, Acciavatti et al. 1992). Criddle (1907) observed that this species is the latest of the Manitoba tiger beetles to hibernate, with some individuals remaining active until October 21, after several heavy frosts. Burrows descended to 41 cm in sand, and 18 cm in clay, with 148 burrows excavated. He also made the remarkable discovery of *C. duodecimguttata, C. repanda*, and *C. tranquebarica* adults all hibernating in the same burrow. Manitoba collection dates occur each month from April to October.

Remarks: It takes some experience to be able to correctly identify flighty *C. duodecimguttata, C. repanda*, and *C. hirticollis*, although the latter is now quite rare in Manitoba. The author has occasionally found a *C. duodecimguttata* a great distance from water (e.g., sand dunes in the Carberry Sandhills) and believe this may be due to natural dispersal, or being carried by the wind. These factors help explain how isolated pockets of habitat appear to be rapidly found and populated by tiger beetles. Blatchley (1910) and La Rochelle (1977) report this species taken at lights on occasion, so the species may occasionally be active after dark.

Larvae of *C. duodecimguttata* (and other tiger beetle species and caterpillars) have been observed to rapidly flex and arch their bodies when disturbed or pinched, an act which causes them to jump or roll away from the site of disturbance. This is thought to be an adaptation to avoid a predator or parasitoid wasp sting (Harvey and Acorn 2019).

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Apparently Secure. Recommendation: Secure.

Brust and Reese (2020) and their fellow tiger beetle enthusiasts have noticed a decline in this species since the 1990s in the region of Minnesota, Wisconsin and southern Ontario. This is something to monitor locally in the coming years, for a similar decline and loss of populations have occurred in another shoreline species in Manitoba – *Cicindela hirticollis.*

Bio-Fact: Maximum flight speed of a flying tiger beetle has been recorded at 3 m/sec, with an average height of 50 cm and a distance of 5 m. The elytra, held out nearly horizontally, provide aerodynamic stabilization, while the flight wings beat at a frequency of around 100 per second (Nachtigall, W. 1996. Take-off and flight behavour of the tiger-beetle species *Cicindela hybrida* in a hot environment (Coleoptera: Cicindelidae). Entomologia Generalis 20(4): 249-262.)

(© Larry de March)

Big Sand Tiger Beetle (*Cicindela formosa* Say, 1817)

Description: This is one of North America's largest and most-robust tiger beetles (14-21 mm), and populations in Manitoba exhibit dark-brown to red-brown elytra with full and wide cream-coloured maculations. The underparts are bright metallic green with coppery reflections. The humeral mark is short and rounded. Manitoba specimens have heavier maculations than typical *C. f. generosa,* leading Wallis (1961) to have recognized Leng's early description of it as a distinct subspecies, *C. formosa manitoba* Leng, 1902 (type locality Aweme, Manitoba). Criddle (1907) considered the form *Cicindela formosa manitoba* not well differentiated from *C. f. generosa*. However, some reseachers (e.g., Acorn 2004, Spomer et al. 2008) still believe that because of the consistency of the heavy white markings throughout its range, '*manitoba*' should be considered a valid subspecies. Pearson et al. (2015) retained the name *Cicindela formosa generosa* Dejean, 1831, for Manitoba populations, and considered '*manitoba*' a synonym.

Similar Species: The only species likely to be confused with *C. formosa* in the same habitat is *Cicindela lengi.* The latter is a smaller (12-15 mm), narrower, and with similar but thinner maculations, and a longer humeral mark. Manitoba specimens of *C. lengi* also tend to have redder elytra.

Distribution: *Cicindela formosa* is found over a wide range from southern-most parts of Alberta to Quebec, and south to New Mexico and Texas to Alabama. It is absent from the American Southwest and Southeast (Pearson et al. 2015). In Manitoba, it is found only in the southern region as far north as Mars Hill Wildlife Management Area, Patricia Beach on Lake Winnipeg, and Drifting River southeast of Duck Mountain Provincial Park (Lawton 2018, and author observations).

Habitat: This species is common in sparsely vegetated sand dunes, sandy blowouts, sandy glacial-till deposits, and sandy roadsides, which are typical habitats throughout its broad range (Criddle 1907, Wallis 1961, Pearson et al. 2015, personal observations). It is not associated with water, but does inhabit dunes within sight of the water's edge. Dwelling in a site with loose shifting sand, one would expect the larval burrow to repeatedly fill up with wind-blown sand grains. However the beetle cements the top of the burrow with saliva, and its flat head, when in position at the entrance, prevents excessive sand from falling in (Shelford 1908). This is another sand-dependent species whose range was likely more extensive in past centuries, before succession of prairie and forest on ancient barren dune fields and glacial till deposits, following the retreat of Glacial Lake Agassiz in Manitoba.

Activity Period: This is a spring-fall species, overwintering in both larval and adult stages (Shelford 1908, Dunn 1981, Graves and Brzoska 1991, Acorn 1991). Adults emerge in the late summer to feed, then hibernate over the winter. These emerge in spring, and with most mating and egg laying occurring in June and July (Hamilton 1925, Acciavatti et al. 1992). Criddle (1907) noted that the new brood appears about the second week in August in southern Manitoba, and is overlapped by the old brood for about 10 days. Shelford (1908) stated that; "The adults of a given generation are not found so abundantly in the fall and summer as in the spring, and it is probable that many remain over winter in the pupal cavities." The life cycle is two to three years, with the larval stage lasting 24 months, and the adults about 12 months, including their winter period in hibernation (Hamilton 1925, Dunn 1981).

This is the last species to appear in the spring and one of the earlier species to hibernate in Manitoba. Overwintering burrows may descend from 127-200 cm into the sand, which are among the deepest of all North American species of tiger beetles. Owing to this great depth and resultant cold ground in the early spring, some individuals appear as late as late May (Criddle 1907, 1910). Manitoba collection dates are from April to September. In late summer, one frequently comes across specimens reluctant to fly and which could be captured easily by hand. Most of these also display dark patches on the elytra, both signs of aged individuals.

Remarks: The author found this species common or abundant in many locations, sometimes observing a dozen in view at a time, and over 100 in a day of hiking through the Carberry Sandhills. It is sometimes especially wary and often flies out of sight when disturbed, frequently accompanied by a loud buzzing generated by the wings, which distinguishes this species in the field in Manitoba. It is usually found in association with the smaller *Cicindela scutellaris* and *C. lengi*. Pearson and Vogler (2001) concluded that of the 111 species of North American tiger beetles for which they had range maps, the two species whose distributions are most similar were *C. formosa* and *C. scutellaris*, being sympatric in, and restricted to, dry sand dunes and sandy blowouts. The large difference in size between the two species, and hence prey focus, are likely involved in their avoiding competition for prey.

Remarkably, Acorn (1991) observed *C. formosa* feeding on adult *Cicindela limbata* and *Ellipsoptera lepida* in Alberta, and it likely pursues and devours on occasion the other species of tiger beetles with which it comes into contact in Manitoba. The author has not witnessed such an attack, and most attempts probably prove futile when considering the speedy flight of the smaller species.

Criddle (1907, 1915) described in great detail the burrow structure and excavation technique of larval *C. formosa*. "Other species [of tiger beetles] have nearly a straight hole usually at right angles to the surface, but *manitoba* constructs a cup-like pit into which the burrow enters horizontally from one side and then gradually curls downwards to a perpendicular position. The advantage of this is that it forms a regular death trap to the unsuspecting insect which happens to be crawling near. Possibly this simple method of procuring food is at least in part responsible for the larger size of the species." He experimented by throwing small ants into the pit, which were captured while endeavoring to make their way out. When the ant reached the bottom of the steep incline, the larva emerged fully from the burrow and secured the ant so rapidly that Criddle could not follow the action. Such a speedy attack would greatly increase the frequency of success, since a greater variety of arthropods (e.g., especially fast flyers like flies) would fall prey.

The author watched an adult *C. formosa*, which was sitting on top of a pocket gopher mound, detect, run after, and attack a large, fast-crawling caterpillar on a sand dune. Over the next minute, the beetle repeatedly bit its prey, but surprisingly, finally gave up and let the caterpillar escape; perhaps it had a toxic taste, or the beetle was deterred by the caterpillar's dense covering of long setae. A colleague Reid Miller observed a *C. formosa* attempting to devour a *Cremastocheilus retractus* ant scarab in the Carberry Sandhills, but the attack was futile, likely due to the latter's tough integument (an adaptation to foil the bites of ants). This largest species of tiger beetle in Manitoba has long been known for its powerful flight. As early as 1910, Blatchley noted; "It is more wary and difficult to capture than most of its kind and when flushed it makes a profound flight." The author has repeated 'pushed' an individual to test its avoidance behaviour, and after two or three flights, the beetle usually flies all the way back to its first location, or seeks cover in nearby vegetation.

This species has five recognized subspecies which display great colour variation (Pearson et al. 2015). Many years ago the author collected specimens of the isolated subspecies *C. f. gibsoni* in the sandhills of Saskatchewan and northwestern Colorado, which have greatly expanded white maculations (elytra are mostly white). Recently, French et al. (2021) assessed genetic differences (mitochondrial and nuclear markers) between these two populations, separated by 1100 km, and concluded that the Colorado population merits distinct subspecies status, *C. f. gaumeri* ssp. nov. The two may have evolved a similar elytral pattern independently, or have been separated from a common stock for many thousands of years. Both are now threatened subspecies.

In southern areas of the United States, the author has also collected samples of other isolated subspecies that are a beautifully rich, reddish-purple colour with few or no white maculations (e.g., *C. f. rutilovirescens* and *C. f. pigmentosignata*). Given sufficient time (i.e., many thousands of years), these disjunct subspecies, with no chance of interbreeding, could potentially evolve into distinct species.

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Critically Imperilled (an obvious error). Recommendation: Secure.

The largest population in Manitoba is presently secure within the Spruce Woods Provincial Park, and the author and others have located multiple additional populations across extreme southern Manitoba. The western race, *C. g. gibsoni,* in Saskatchewan and Alberta has been assessed as Threatened by the Committee on the Status of Endangered Species in Canada, due to multiple factors, but mainly to dune stabilization from plant succession (Bell et al. 2019). NatureServe lists this subspecies as Critically Imperiled. The same factor of plant succession has certainly reduced the size, distribution and number of populations of *C. f. generosa* (and other tiger beetle species) in southern Manitoba, which is why the author, in his permit reports for research in provincial parks and protected areas, has for years stressed the importance of reversing plant encroachment on the ever-diminishing, semi-open dune complex of Spruce Woods Provincial Park.

TIGER BEETLE ON THE DUNE

When I spot a beetle and it sees me,
I know more about it, than it knows me.
But for the chances of our DNA,
it could be me, sitting high on the sand
on six spindly legs, watching with bulging eyes
the two-legged giant approaching, net in hand.
Yet with all my abilities and visual/brain power,
I cannot follow the beetle's fleet flight,
carrying it to safety in a concealed site
in the nearby grassy bower.

Robert E. Wrigley

(© Larry de March)

Crimson Saltflat Tiger Beetle (*Cicindela fulgida* Say, 1823)

Description: This is a small (10-12 mm), narrow-bodied tiger beetle of variable colour (coppery, brown, red, green, purple, or blue), with broad white markings, finely pitted wing covers and pronotum, and a shiny, somewhat greasy appearance. The humeral (front) and middle lunule are sometimes united along the outer elytral edge. Wallis (1961) described *Cicindela fulgida westbournei* as slightly smaller, less brilliant, with heavier maculations, and with slight differences in lunule spacing compared to the nominate subspecies *C. f. fulgida* in adjacent North Dakota.

Similar Species: No other Manitoba tiger beetles closely resembles *C. fulgida*.

Distribution: This species occurs in often-isolated saline/alkaline sites from southern Alberta to Manitoba, and south through the central states to the northern regions of Arizona, Texas, and Oklahoma. In Manitoba, it is restricted to the extreme south-central and southwestern parts of the province in the former mixed-grass prairie region. The author has studied the population several kilometres north of St. Laurent for a number of years, and Lawton (2018) subsequently found it 45 km farther north at Eriksdale, along Highway 6, its current northern limit.

Habitat: The author has recorded populations in Manitoba on sparsely vegetated patches of saline clay soil along roadside ditches, and on a clay/gravel edge of a nearby dugout pond (i.e., mostly artificial habitats). It is likely that many natural saline sites on the prairie were once occupied by this species, but these have mainly been destroyed when most of southern Manitoba's prairie was converted to farmland and grazing livestock. This species is typically restricted to open, wet or dry, saline habitats by streams, ponds, coulees, sloughs, and badlands (Wallis 1961, Willis 1967, Hilchie 1985, Pearson et al. 2015). The latter concluded that this species selects sites; "...where high summer temperatures result in constant evaporation and concentration of high pH (8.5) minerals on the soil surface."

When searching for populations of this species, the author looks first for low-growing patches of Red Saltwort (*Salicornia rubra*) and Alkali Grass (*Distichlis spicata*), particularly along roadside ditches, and the edges of sloughs and creeks, for they are characteristic of the Crimson Saltflat Tiger Beetle's habitat.

Activity Period: Adults emerge from pupae in late summer and fall, enter hibernation by September, emerge the next spring, feed and mate, then die out in the summer (Wallis 1967). Spomer et al. (2008) and Pearson et al. (2015) described this as a spring/fall species, with adults active from April to June, and from July to October in the United States. Manitoba collection dates are from late May to early September, with a population peak in June and July. Hilchie (1985) also reported adults from early spring to late fall in Alberta. Little is known about larval biology. Criddle (2010), quoting J. B. Wallis, stated; "Specimens were taken during the middle of August, and the species will probably be found to hibernate not at any great depth."

Remarks: *Cicindela fulgida westbournei* was originally named *Cicindela fulgida elegans* by E. E. Calder, but the name was preoccupied, and so it was changed the same year. Criddle (1910) quoted J. B. Wallis, who collected the type specimen; " I took *fulgida* on what is known at Westbourne as the Salt Plain, an alkaline stretch of some extent. The plain is in the main fairly well covered with loosely-growing wiry grass, with fairly numerous bare or nearly bare patches of soil sufficiently alkaline to be more than grey. Here *fulgida* was plentiful in company of *tranquebarica*."

The type locality is probably 11 km W of Westbourne, as there appear to be no other salt plains in the area. From 1966 to 1983, an auto racetrack, known as the "Salt Plains Stockcar Raceway," operated on the site. After the raceway closed, the area became pastureland. Despite extensive habitat disturbance while the racetrack operated, limited salt plain habitat remained on the site and in the roadside ditch bordering Highway 16. The author and Colin Hawkins collected 11 specimens there up to 1996. Subsequent surveys by the author and others have failed to locate any individuals, and plant succession has left few open salt patches. It appears that *C. f. westbournei* is now extirpated at the type locality.

The author found this species particularly challenging to follow its flight path to its landing spot (often among vegetation), and to collect, due to its small size and fast, low flight. Criddle (1910) noted; "This species is of strong flight, readily passing from one bare spot to another." Willis (1967) observed that it is normally found among sparse vegetation, usually flies at the slightest danger, often into dense vegetation, but sometimes out onto a bare salt flat. The larva was described in detail by Willis (1967), and larval microhabitat consisted of "small flats, near margin" and "near hummocks, among vegetation," the latter being the most frequent. He reported active larvae and swarms of adults in areas that had been recently flooded, indicating this species survives episodes of flooding.

Dr. Terry Galloway first observed *Cicindela fulgida* on the open salt patches in the roadside ditch on Highway 6, several kilometres north of St. Laurent (at the time the northern-most record in the province). On June 25, 2000, the author checked the location and found the species remarkably abundant (along with 5 *Parvindela terricola*), numbering in the hundreds on a connected series of patches of wet, salty, packed mud. A dozen individuals were observed on the clay/gravel shore of a nearby pond. Perhaps the construction of the highway ditches in the 1950s created suitable habitat for the species, allowing it to extend its range northward. The author checked on this local population periodically over succeeding years, and found only small numbers or none at all in early summer. The ditches are susceptible to spring flooding and intense heat and aridity in summer, so likely conditions are not always conducive to support survival of immature stages and adults. ATVs and snowmobiles, commonly operated in the area summer and winter, may also have negative impacts on adults and larvae at different times of the year (e.g., soil compaction in summer, lower ground temperature from loss of snow cover). These factors may also restrict the invasion of salt-tolerant grasses and Red Saltwort onto the clay flats.

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Unrankable. Recommendation: Special Concern. No populations are located in protected areas, known populations are sporadically distributed and subject to disappearance (e.g., at the type locality) from encroachment of vegetation, agricultural developments, and exposure to chemical spraying for weed control.

The Crimson Saltflat Tiger Beetle is restricted to open or sparsely vegetated salty patches, often found in roadside ditches. Before roads and drainage ditches crisscrossed southern Manitoba, this species likely inhabited extensive natural salt flats along the edges of sloughs, marshes, rivers, and lakes, kept clear of vegetation by drought and high salt content of the soil. This species is often observed in the company of the Variable and Oblique-lined tiger beetles. If a beetle was spotted on the open, white, crusty area in the above photo, an observer or predator would have no chance of finding it again once it darted into the adjacent plant cover. (© Larry de March)

(© Larry de March)

Hairy-necked Tiger Beetle (***Cicindela hirticollis*** Say, 1817)

Description: This is a medium-sized (10-16 mm), dark-brown species featuring bold and complete maculations. The humeral (shoulder) lunule is recurved into a 'G' shape, and the middle lunule is long and sharply elbowed. The posterior ends of the elytra are pointed. True to its name (i.e., *hirticollis,* Latin meaning hairy neck), *Cicindela hirticollis* sports a large brush of white setae on the neck (thorax). Some of these hairs are worn down or are lost from abrasion. This species demonstrates sexual dimorphism, with the male being smaller and relatively narrow compared to the female.

Similar Species: *C. hirticollis* closely resembles *C. repanda* and *C. duodecimguttata,* but may be differentiated by the humeral (shoulder) lunule hook of a 'G' in *C. hirticollis*, compared to a 'C' in *C. repanda*, and lack of a substantial humeral lunule in *C. duodecimguttata.* The latter two also lack the prominent brush of white setae on the thorax. It takes a trained eye to distinguish the three species from a distance, but is readily accomplished in the hand.

Distribution: This attractively patterned species occurs over much of North America, from British Columbia and Newfoundland south to California and Florida, and even into Mexico (Cazier 1954, Pearson et al. 2015). In Manitoba it is known only from a small number of sites in southern and central parts of the province. Lawton (2018) recorded it recently as far north as Minago River, northwest of Jenpeg, a range extension northeast of 350 km.

Habitat: This tiger beetle usually prefers barren sandy beaches (often with dunes nearby) of rivers and lakes, but is occasionally found in other sandy unvegetated habitats, near or far from water (Wallis 1961, Hilchie 1985, Graves

1988, Acciavatti et al.1992). Larvae occur in burrows in moist sand above the level of wave action. Moisture of the burrow is quite critical, with the sand being neither too moist or dry (Graves 1963). Willis (1967) found it in fluvial mesic and saline habitats. Preston trapped one specimen on a sandy public beach beside a pond in a campground in Spruce Woods Provincial Park, Manitoba. The author found four individuals on August 30, 2007 at Grand Beach Provincial Park, at the southern end of Lake Manitoba, in association with numerous *C. repanda*. The site was a sandy slope of a lagoon separated from the lake by dunes. Lawton (2018) found abundant *C. hirticollis* on a little-disturbed sandy beach at Elk Island Provincial Park, on the mainland beach north of Victoria Beach, and in a wet sandy roadside ditch in northern Manitoba.

Activity Period: This is a spring/fall species, with adults becoming active later in the spring than most other species. New adults emerging from pupation in July overlap with year-old adults, which die off by late August. The former then hibernate and become active the following spring, when they soon mate and lay eggs (Shelford 1908, Acciavatti et al. 1992). Larval stages take one to three years before pupation, depending on food supply and latitude. Three years are likely required in Manitoba. The burrows occur in moist sand to a depth of 15-20 cm along beaches. Excessively dry or wet conditions cause the larvae to abandon their burrows, and to search up or down the beach for situations with acceptable moisture content (Shelford 1908, Knisley and Schultz 1997). It is therefore up to the egg-laying female to select oviposition sites that are high enough above the flooded zone, and yet placed not so exposed on the beach that excessive summer heat and aridity cause the death of the egg or larvae. Manitoba collection dates: May to October.

Remarks: Many researchers have commented on this species' sensitivity to disturbance by humans, through various kinds of shoreline alterations (Graves 1988, Graves and Brzoska 1991). Pearson et al. (2015) concluded that; "Probably because of its narrow range of moisture tolerance, this species is susceptible to droughts, pollution, pesticides, river damming, channelization, shoreline development, and destruction of larval habitats by vehicles and other human-caused modifications of its habitat. The species has disappeared from many of its former haunts in New England and the Midwest." Knisley and Fenster (2005) concluded that the subspecies *C. h. abrupta* of the Sacramento Valley in California is now extinct due to shoreline habitat destruction by dams. On the positive side, the current author has often come across large populations along many sandy river shorelines in the central United States.

This is a rare species in Manitoba that should be watched for on sandy lake shores and river banks throughout the province. There are a few old (1923) records of this species along the sandy shore of Victoria Beach, but with major cottage development and subsequent decades of heavy foot traffic from crowds on the beach, the species is scarce or no longer occurs along great stretches of shoreline. On nearby Elk Island Provincial Park, with few visitors and no development, the species is still common, perhaps the most-abundant surviving population in the province.

This species is almost aways found in the presence of *C. repanda* and sometimes *C. duodecimguttata* on beaches. The beetles' high level of activity along the wet margin of the shore would presumably expose them to significant predation by shorebirds.

The larva of the Hairy-necked Tiger Beetle differs significantly from other species in the frequency of appearence on the surface in order to relocate a burrow due to flooding (a not-uncommon occurrence in its streamside habitat) or aridity (7-50% saturation is preferred) (Shelford 1908, Brust et al. 2006).

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Not Ranked. Recommendation: Threatened. This is due to the limited number of occurrences, high susceptibility of elimination by human activities, and subsequent loss of populations. Manitoba is at the northern periphery of the species' wide range, and the relatively short summer period of activity translates to a lengthy lifespan (possibly up to four years for some individuals), spent mostly in hibernation. This long period before breeding increases susceptibility to predation and other causes of mortality, which is possibly a factor in why populations are so few and numbers so low in the province.

Beach habitat of the Hairy-necked Tiger Beetle north of Victoria Beach on the southeastern shore of Lake Winnipeg. Heavy foot traffic arising from nearby cottage developments has reduced the survival of the beetle's larval stages by collapsing their burrows. In the distance is Elk Island Provincial Park, whose little-visited sandy shoreline perhaps hosts the largest surviving population of this rare beetle in the province.
(© Larry de March)

(© Larry de March)

Blowout Tiger Beetle (*Cicindela lengi* W. Horn, 1908)

Description: This is a medium-sized (12-15 mm), parallel-sided, attractively patterned tiger beetle with full and heavy maculations, resulting in about 50% of the elytra being white. In Manitoba the dorsal colour is bright red to brownish red (sometimes with a green reflection), the venter is bright green, and the sides of the pronotum are coppery. The humeral mark is long and oblique. The subspecies *Cicindela lengi versuta* occurs in Manitoba (Wallis 1961).

Similar Species: Two species might be confused with *Cicindela lengi* in Manitoba. *Cicindela tranquebarica* is broader, mainly dark brown, the humeral mark is longer and oblique, and the markings are not connected along the margin. In the more-robust *Cicindela formosa,* the humeral maculation is short and rounded.

Distribution: *Cicindela lengi* occurs in sandy sites over most of Alberta and Saskatchewan, and in southwestern Manitoba, and then south to the northern parts of Arizona, New Mexico and Kansas (Pearson et al. 2015). It has been recorded as far north as 5.6 km west of Barrows on Highway 77 (Lawton 2018).

Habitat: This species is confined to partially vegetated sand dunes and flats in prairie, and sandy trails along Jack Pine ridges in boreal forest (Wallis 1961, Hilchie 1985, author's observations). Criddle (1907) noted that favoured habitats are dry sandy fields and small blowouts in which there is some vegetation. Acorn (1991) found it to be most common in dune margins and pioneer vegetation areas. Some authors (Spomer et al. 2008) have reported it along sandy creek banks, but no such instance has been noted in our province. The author consistently found this species present over the decades along a sandy trail through arid mixed-grass/juniper prairie that leads to the Bald Head Hills in the Spruce Woods Provincial Park – possibly hosting the largest population in Manitoba.

Activity Period: This is a spring-fall species, requiring up to three years to complete larval development (Hilchie 1985). Overwintering occurs as adult and larva (Acorn 1991). In Manitoba, Criddle (1910) reported this species throughout the warm season, with the old brood beginning to disappear about the middle of July, and the new cohort appearing in early August. Larval and adult burrows are situated in sandy soil on either flat and sloping sites, and descend to 30-130 cm, averaging 50 cm (Criddle 1907, Pearson et al. 2015). Manitoba collection dates: April to October.

Remarks: The type specimens of the formerly recognized *Cicindela venusta versuta*, described by Casey in 1913, were collected at Aweme in southern Manitoba by Norman Criddle. Criddle (1907) noted this species was a strong flier, though not quite as strong as *C. formosa*. The author concluded that where one finds *C. lengi,* it is likely that *C. formosa* and *C. scutellaris* will also be present (e.g., in the Bald Head Hills of Spruce Woods Provincial Park). Surprisingly, however, he never found it invading the major dune field, preferring to remain along sandy trails with vegetation alongside. Pearson et al. (2015) noted that *C. lengi* can persist in smaller pockets of sand longer than most other species of tiger beetles, and is often the last to disappear as vegetation encroaches on the site.

The author observed that this species is relatively easy to approach and collect, since it usually flies a short distance further along the trail, rather than immediately seeking cover in adjacent thick vegetation.

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Vulnerable. Recommendation: Vulnerable. It occurs only in small populations in a few localities. While generally considered an uncommon species, on occasion it may be locally common in the Spruce Woods Provincial Park, and consequently this particular population is secure.

(© Larry de March)

Common Clay Bank Tiger Beetle (*Cicindela limbalis* Klug, 1834)

Description: This is a medium-sized (11-16 mm) tiger beetle with brilliant red, dull reddish-green, or purplish elytra, and prominent maculations. There is a subhumeral (shoulder) spot, and the middle lunule comes close to or meets the outer and inner edges of the elytrum.

Similar Species: Due to their close relationship, *Cicindela limbalis* closely resembles *C. purpurea,* as they are both the same size, have similar maculations, and may have green or dark red elytra. The middle lunule of *C. limbalis* is broader, longer (i.e., reaches close to both the outer and inner edges of the elytrum), and is shaped like a 'knee and foot.' Generally a post-humeral dot is present in *C. limbalis* and absent in *C. purpurea*.

Distribution: This attractively coloured species occurs from the Northwest Territories to Newfoundland and Cape Breton Island south to New Mexico, Missouri and Pennsylvania (Pearson et al. 2015). It is found over the southern two thirds of Manitoba.

Habitat: This beetle is usually found on steep clay banks with limited vegetation (Wallis 1961, Graves 1963, 1965, Dunn 1981, Hilchie 1985). Hilchie (1985) collected specimens along the margins of a slough in Alberta, and Criddle (1907) noted its presence along roadways and riverbanks, and on pocket gopher mounds in southern Manitoba. The author located a small population along a dusty road inside Winnipeg's Assiniboine Park Zoo, adjacent to the silt-covered shore of the Assiniboine River – the likely source of immigration. James Duncan (personal communication) collected one on a mound of earth at a fox burrow. Collin Hawkins (personal communication) found most specimens on flat areas (e.g., old road construction sites not yet grassed over), and north of Thompson, he recorded it on a Jack Pine-covered gravel hill. Although this species prefers a clay substrate, he also observed it on salt flats.

The author noted over many years that *C. limbalis* and *C. denikei* occurred together along two trails in spruce-poplar forest west of Rennie, at the base of a grassy clay slope, and a muddy-clay, heavily rutted road kept open by occasional passing vehicles. At both sites, encroaching grasses (i.e., less open ground) appeared responsible for decreasing numbers of individuals over the years. He observed that when disturbed, this species is a strong flyer, rapidly heading into grass to escape, and can therefore be very difficult to relocate due to its camouflaging colour and pattern.

Activity Period: Adults are active in the spring and fall (Dunn 1981, Wilson and Brower 1983), the culmination of a three-year life cycle (Hilchie (1985). The larva passes the first winter in the second larval stage (Shelford 1908). The new cohort of adults emerges from pupae in August (Criddle 1907). Larval burrows are usually situated at the base of a clay bank (Hilchie, 1985; Wilson and Brower, 1983), and the larva often constructs a chimney-like structure about 6 mm high around the mouth of the burrow from clay particles excavated from the bottom of the burrow. A burrow descends to about 15 cm deep, almost horizontally into the bank, and with a side pupal chamber near the bottom of the burrow (Shelford 1908). Manitoba collection dates: April to September.

Remarks: The author and other researchers (Pearson et al.) found this species somewhat solitary, finding only one to five specimens at any one location. This habit is quite in contrast with its close relatives, *Cicindela purpurea* and *C. denikei*, which may occur in large numbers. Its late emergence in spring also differs from early emerging *C. purpurea*.

At one site in the boreal forest, which the author checked each spring, he noticed a crack in the ground (a hibernaculum) from which emerged a number of Red-sided Garter Snakes (*Thamnophis sirtalis*). He wondered whether the snakes were able to prey on the local *C. purpurea* and *C. denikei.*

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Unrankable. Recommendation: Secure.

Pearson et al. (2015) noted that this species has been extirpated from most of southern New England, a highly developed region. For example, it has been designated Vulnerable in Vermont and Special Concern in Massachusetts due to; "Bank stabilization activities that disrupt the natural regime of erosion and deposition that create and maintain its dynamic habitat" (Massachusetts Natural Heritage and Endangered Species Program 2012). The potential loss of populations should be monitored in southern Manitoba, where mixed-grass prairie has been and continues to be highly modified for agriculture and other developments.

(© Larry de March)

Sandy Tiger Beetle (*Cicindela limbata* Say, 1823)

Description: *Cicindela limbata* is a small (10-12 mm) species with wide, creamy-white maculations (over 85% white elytra in the southern *C. l. nympha*) and dark legs. This species is remarkable for the dense tufts of long white setae liberally distributed on the head, thorax and undersides, although they are often worn off the abdomen of older individuals from the abrasive action of sand. In the subspecies *C. l. nympha,* the dark areas are restricted to the elytral suture and a dash paralleling the outer margin towards the apex. Aweme (north of Treesbank), Manitoba is the type locality for this subspecies. *C. l. hyperborea,* in far northwest Manitoba, is the darkest and smallest of the subspecies, with heavy brown maculations (Pearson et al. 2015).

Similar Species: This tiger beetle resembles the Ghost Tiger Beetle, *Ellipsoptera lepida,* but it has browner, more-defined markings, especially along the elytral suture, than the latter species, and the legs are dark, not white. Both species have dense patches of setae on the forequarters.

Distribution: This species occurs in widely disjunct populations. In Canada, it is found in Alberta, Saskatchewan, adjacent Northwest Territories, and western Manitoba. There is a remarkable record in Wapusk National Park, near Churchill on Hudson Bay (Woodcock et al. 2010), and Lawton (2018) found individuals at Mafeking and Lynn Lake. It probably occurs in other scattered locations across the central and northern regions of the province. A disjunct population was reported in Labrador, almost 3000 km east from its nearest neighbouring population in Manitoba.

In the United States, the species has also been located in isolated sites in Montana, Colorado, Wyoming, Nebraska, the Dakotas, and another in northwestern Alaska, 2600 km northwest of the next population in the Northwest Territories (Pearson et al. 2015). Such a grouping of distantly isolated populations signifies a once-wide ranging distribution on open sand habitats that have become fragmented during the current phase of decreasing temperature and increasing moisture following the Holocene Climatic Optimum, which lasted from 6000 to 3000 years ago. The beetle's preferred habitat of open sand deposits and dunes, with only sparse vegetation, would have been far-more widespread prior to the succession of plant communities over the recent millennia. Five subspecies are recognized, two of which, *C. l. nympha* and *C. l. hyperborea,* occur in Manitoba (Pearson et al. 2015).

Habitat: This is a species of sandy sites, generally not associated with watercourses. The author has found two populations of this species in Manitoba – in the Carberry Sandhills and at the southern limit of the Portage Sandhills west of St. Claude. Criddle (1907, 1910) noted that it abounds on large sandy plains and blowouts where vegetation is scanty, and is more plentiful on white sand that is constantly drifting. Others have located populations in sandy blowouts on Jack Pine ridges in the boreal forest (Wallis, 1961). In northern Manitoba, Lawton (2018) found individuals along roadsides, and in gravel and sand pits. In northern Saskatchewan, this species was reported on the beaches of Lake Athabasca, at the northern limit of the species range (Acorn 1994).

Activity Period: Criddle (1907) noted that this is one of the first species to appear in the spring in Manitoba, as early as April 3 (right after snow melt), and he observed some individuals active into late October. He found groupings of up to a dozen eggs in an area of only 77 sq cm during the mating season in June and July. Toward the end of July, a great many of the over-wintering adults died off, but some remained active until the new brood appeared during the first and second week of August. Pupae were uncovered on August 11. By the end of August and into September, the new adults commence excavating their hibernacula, which descend an average of 28 cm (maximum 43 cm); the same depths as the larvae. While some individuals burrowed in the middle of blowouts, most preferred the sloping edges close to vegetation. Remarkably, he discovered one larva still digging its burrow as late as October 26, 1906, when the surface of the ground was frozen. Both adults and larvae overwinter (Acorn 1991). Criddle (1910) and Hamilton (1925) determined the species has a three-year life cycle. Manitoba collection dates are from April to October.

Remarks: Criddle (1907) stated this to be one of the most abundant of our tiger beetles on the edges of open dunes and large sandy blowouts. The author also found this species to be abundant in the same Carberry Sandhills as noted by Criddle, where easily a hundred could be observed in an hour hike along the trails. Local amateur entomologist Collin Hawkins (personal communication), collecting in the Carberry Sandhills and in sand blowouts in Jack Pine forest in the Duck Mountains, noted that *C. limbata* was very difficult to spot on pale sand until it flew, and was challenging to capture due to its alertness, rapid flight, and camouflaging light colouration. He found *C. limbata, C. formosa*, *C. scutellaris*, *C. lengi*, and *C. tranquebarica* in the same habitat, which is in accordance with the author's observations; on many occasions, he has observed the first four species plus *Ellipsoptera lepida* inhabiting the same barren or sparsely vegetated sandy ecotone of the Spruce Woods Provincial Park. Lawton (2018) noted that in central and northern Manitoba, *C. limbata* was often absent from areas that appeared to be suitable habitat. Larochelle (1977) cites a reference to captures at night lights.

Dawson and Horn (1928) relate an interesting anecdote about this beetle. "The beautiful species *C. limbata* was lost to science for a number of years after [Thomas] Say described it [in 1823]. When rediscovered, specimens were so much in demand by collectors and students that several collecting expeditions were financed by the sale of specimens, until the world market was supplied. The "golden days" are past. There is no money in tiger beetles, but these incidents help one to realize the interest that has long been centered upon these attractive insects."

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Not Ranked. Recommendation: Secure.

Human activities may readily eliminate species of tiger beetles from sensitive sand dune and shoreline habitats. For example, *C. l. nympha* was recorded in sand dunes in Polk County, Minnesota in 1967 and listed as endangered in 1996 by the Minnesota Department of Natural Resources (report now dated 2021), but by 1970 it was presumed extirpated from the state because of recreational use, including off-road vehicular traffic, which destroyed the larvae in their burrows (Steffens 2005).

For over a decade, the author observed a small isolated population (estimated at fewer than 40 individuals) on the steep slope of a 10-metre-high sand dune (on private property) on the southeastern-most, periphery of the Portage Sandhills, west of St. Claude, along Highway 2. The site had been kept free of surrounding oak-aspen forest encroachment by the occasional removal of sand by heavy equipment and the steepness of the slope. However, none has been seen for a number of years (only *Cicindela formosa* remains on a nearby sandy roadside and trail), and it appears the population has died out, likely due to destruction of the larvae from renewed sand excavation. It will be interesting to see if the site ever becomes reoccupied in the future. This area is now surrounded by mature deciduous forest and agricultural land (crops and cattle pasture), but there are areas and trails of bare sand in the Portage Sandhills to the north where this species potentially exists.

(© Larry de March)

Long-lipped Tiger Beetle (*Cicindela longilabris* Say, 1824)

Description: This is a medium-sized (12-17 mm) tiger beetle with a distinctively long labrum (upper lip) which is generally white in both sexes. The elytral colour varies from black to brownish bronze, with maculations ranging from bold to absent, but usually only tiny white dots and a slim middle lunule are characteristic. The elytral surface is minutely granular, giving it a dull luster. The abdomen is usually blue-green or green, with purple or coppery reflections, but occasionally black.

Similar Species: It is very similar to *Cicindela nebraskana*, with *C. longilabris* averaging slightly larger (by only 1 mm or less), and often exhibiting heavier maculations. The labrum of *C. longilabris* is generally white in both sexes, the elytra have a dull luster caused by the microsculpture, and the abdomen is usually bright green. The elytra of *C. nebraskana* are typically immaculate and shiny, and the abdomen is black with purple or green reflections. The black phase of *C. purpurea* may be identified by abundant setae on the frons (front) and vertex (top) of the head.

Distribution: This predominantly boreal species occurs throughout Manitoba as far north as Churchill and Wapusk National Park along the coast of Hudson Bay (Woodcock et al. 2010). It has an extensive distribution across North America, from Alaska to Newfoundland, and over much of the West at higher elevations, south to California and New Mexico. Duran (2010) stated that; "*C. longilabris* is extraordinary for its occurrence at extremely high latitudes and altitudes, including areas where no other tiger species exist...from southern Arizona to north of the Arctic circle (Spanton 1988), and an east-west distribution from the coast of Newfoundland to western Alaska (Knisley per. comm. 2006). In the Southwest extent of its range, this species is also found at high elevations up to 3800 m, indicative of its tolerance of cooler climates (Schultz et al. 1992)."

Considering that most species of tiger beetles are temperate and tropical, the adaptations of *C. longilabris* to survive in an extremely cold subarctic climate, find sufficient prey in a short warm season, and ability to find hibernation sites above the permafrost, are truly remarkable. Individuals have been observed active at temperatures as low as 8.5°C (Larochelle and Lariviere 2001), whereas the author's experiences with a number of species of Manitoba tiger beetles indicated a temperature of 14°C was required. This species loses 45% less moisture through its cuticle than species living near watercourses and moist habitats (Hadley 1994).

Habitat: In boreal coniferous forest and boggy areas, *C. longilabris* is found on sandy sites such as ridges, blowouts, and sandy roads (Dunn 1981, Graves 1963, 1965, Hilchie 1985, Wallis 1961, Lawton 2018, the author's observations). It may also be found on mucky, very dark woodland soil (Wilson and Brower 1983). Lawton (2018) discovered this species in abandoned gravel/sand excavation areas, sandy road cuts, forestry roads, and under power-lines in northern Manitoba. Most of the author's specimens were collected on sandy, abandoned forestry trails in Jack Pine or White Spruce-Aspen Popular forests in the southeastern part of the province.

Activity Period: This is a spring-fall species, over-wintering in the larval and adult stages (Hilchie 1985), and with a life cycle of 3 or 4 years (Pearson et al. 2015). Burrows descend to 8-20 cm and the new brood appears from late July to early August (Criddle 1907). Manitoba collection dates: May to September.

Remarks: This species is most commonly observed in Manitoba on sandy paths through coniferous forest, where it basks in the sun, exposing its dark pigmentation, and awaits the appearance of prey. When disturbed, it usually flies from 5-10 metres further along the path, and if repeatedly pushed, it flies back to its original site, or off into adjacent low vegetation and remains stationary, where its dark camouflaging colour make it impossible to detect. It closely resembles a burned piece of a twig.

Lawton (2018) observed that this was the most commonly encountered species in central and northern Manitoba. One year, the author observed up to 50 individuals while walking a few hundred metres along an abandoned, sandy Jack Pine forestry road (Lewis Road south of Highway 15) in southeastern Manitoba. The road had a number of small pools and wet spots present, following a period of rain. Checked annually for over two decades, this population has fluctuated markedly, with abundance appearing to be negatively affected by drought conditions, which simultaneously reduced the presence of other arthropod prey such as ants and caterpillars. The daily period of activity was restricted by the curtailed hours of mid-day sunlight reaching the narrow trail as a result of the deep shade cast by both sides of the tall Jack Pine trees (see page 20).

There has been considerable speculation over the years about the relationship between *C. longilabris* and *C. nebraskana*. Some researchers suggest that they are different species with hybrid zones in locations such as the Black Hills of South Dakota, Manitoba, and the Rocky Mountains. Others hold the opinion they are sister species, or that they are in the process of speciating. Spanton (1988) compared *C. longilabris* and *C. nebraskana* across Canada and the United States and found statistical differences in size and proportion of the labrum (upper 'lip'), and the ratio of the head width to pronotal width, differences in qualitative characters such as female labrum colour, colour of ventral abdominal surface, proepisternum and elytral surface, differences in patterns and extent of markings, as well as ecological separation based on distribution relative to major soil types. He concluded that *C. longilabris* and *C. nebraskana* are distinct species, and that no apparent hybridization occurs in sympatric (i.e., occurring in the same area) populations.

Spomer (2009), working with specimens from Nebraska and the Black Hills area of South Dakota, found that ventral and proepisternal colour, presence or absence of a middle band, and elytral luster were most useful in separating the two taxa. He found that hind tarsal length (that of *C. longilabris* is 0.4-0.6 mm longer) and the labrum width/length ratio were also important diagnostic characters. He concluded that some specimens in low-elevation populations in the Black Hills of South Dakota, which had dorsal colouration of *C. nebraskana* and bright green abdomens and intermediate tarsal lengths were *C. longilabris* x *C. nebraskana* hybrids. Duran (2010, unpublished PhD manuscript) sampled *C. longilabris* and *C. nebraskana* across Canada and the United States, and using multiple molecular analyses, concluded that the two were the same species, with *C. nebraskana* being a widespread variant. Both Spanton (1988) and Spomer (2009) found that there is variation in some of the distinguishing characters of some specimens of *C. longilabris* and *C. nebraskana,* making identification uncertain. The relationship of these two taxa will doubtless continue to attract the attention of researchers.

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Apparently Secure. Recommendation: Secure.

(© Stephen Spomer)

Prairie Long-lipped Tiger Beetle (*Cicindela nebraskana* Casey, 1909)

Description: This is a medium-sized (12-14 mm) tiger beetle characterized by a long labrum and set of mandibles, and with elytra black and immaculate. Occasional specimens show slight white maculations and a middle band. Spanton (1988) reported smooth fields between the elytral punctures, which result in more luster than in *C. longilabris*. The abdomen is black, sometimes with slight purple or green reflections. In males, the labrum is usually white, while in females, black predominates. There are two other forms that occur less frequently in Manitoba. One has a brilliant-green abdomen and dark elytra with a metallic-green tint, a form described by Casey (1913) as *spissitarsis*, whose type locality is Aweme, Manitoba (Wallis 1961). The other form presents brownish bronze elytra, a green abdomen, and a white labrum in both sexes.

Similar Species: See *Cicindela longilabris* account to distinguish this species. The similar-looking black phase of *C. purpurea* has prominent setae on the vertex and frons (top and front of the head).

Distribution: This species occurs from the extreme southwest portion of Manitoba to British Columbia and south in the western states to North Dakota, Colorado, Utah, and California at high elevations (Pearson et al. (2015).

Habitat: *C. nebraskana* inhabits short- and mixed-grass prairie on heavy clay soil, never on sand (Wallis 1961). Collin Hawkins (personal communication) found it in Manitoba on clay and dried mud in or near grass in open farmland, and along roadside ditches next to a hayfield, sometimes extending into aspen-oak woodland with patches of grass. Hilchie (1985) noted that in Alberta it prefers bare areas between clumps of grass and earth mounds made by ground squirrels. Criddle (1907) noted it on bare spots on dark and dryish land, ploughed fields, and roadways, but nowhere plentifully. Winton (2010) reported specimens in August and September in the Centennial Sandhills of southwestern Montana in sandy sites with high levels of organic matter, supporting grasses and herbs. While mainly a species of mixed- and short-grass plains, some populations exhibit remarkable adaptive physiology in that they have been reported above 2700 m in the mountains of California, at which elevation the growing season is exceptionally short.

Activity Period: This is a beetle with a spring-fall life cycle, over-wintering in both larval and adult stages (Hilchie 1985, Kippenhan 1996). The new brood appears towards the end of July and the beginning of August (Criddle 1907). The larvae probably require two years before pupation (Acorn 2001), consequently the species has at least a three-year life cycle (Brust and Hoback 2005). Manitoba collection dates: May to September.

Remarks: *C. nebraskana* is usually rare and localized in Manitoba, but can vary in abundance from year to year. When disturbed, this beetle usually flies a long distance from the path into the prairie grasses (Criddle 1907, Spomer et al. 2008). With the conversion of mixed-grass prairie to agricultural use in Manitoba, this species, along with others, has likely been negatively impacted. In the United States; "[The] Population is relatively stable but is probably suffering an overall decline because of habitat loss..." https://fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5329010.pdf (accessed 28 March 2020)

See the account *Cicindela longilabris* for comments about the species status of *C. nebraskana.* Pearson et al. (2015) treated it as a widespread variant of the former species.

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre did not list this species. Recommendation: Secure.

Bio-Fact: While females of some species of tiger beetles lay eggs while at the soil surface by probing 5-10 mm with the ovipositor (e.g., *Cicindela purpurea, C. nevadica, Cicindelidia punctulata*), others lay eggs while inside a burrow (e.g., *Cicindela fulgida, C. scutellaris, C. tranquebarica, C. formosa*) at depths of 20-60 mm. Soil-moisture preference may be a determining factor among the species (Brust et al. 2012).

Tiger beetles, like other flying insects, generate considerable body heat, which must be dissipated (e.g., by seeking shade) to maintain their optimal body temperature. Insects have thermoreceptors lining their antennae.

The highly reflective, green/blue, miror-like abdomen, exposed when the beetle takes flight, may momentarily startle a predator, giving the beetle a slightly improved chance of escaping.

(© Larry de March)

Cow Path Tiger Beetle (*Cicindela purpurea* Olivier, 1790)

Description: This is a medium-sized (12-16 mm) tiger beetle which ranges in colour from reddish to green (the latter more common in Manitoba), and with elytral markings reduced to an isolated middle lunule and one or two dots at the rear of the elytra. The middle band is a rear-angled line which approaches, but does does not reach, either the inner or outer elytral margins. Wallis (1961) pointed out the highly variable maculations in local populations. Pearson et al. (2015) listed an eastern *C. p. purpurea* and western *C. p. audubonii* in Manitoba. A black form, '*nigerrima'* Leng, 1919, also occurs rarely in the province. The author has collected only two of these among over 200 specimens.

Similar Species: *C. purpurea* and *C. limbalis* closely resemble each other, and each may have green or dark red elytra. The shorter (i.e., not meeting the outside edge of the elytrum) and more oblique middle band of *C. purpurea* distinguish it from *C. limbalis*. The latter generally has a post-humeral dot, typically small or absent in *C. purpurea*. The black form of *C. purpurea* may be confused with *C. nebraskana* or *C. longilabris,* which are also dark, but the latter two species lack the white apical spot on each elytrum, and have bald foreheads (Acorn 2001).

Distribution: *Cicindela purpurea* is found in extreme southern Canada from British Columbia to Nova Scotia, and over much of the United States, except the Great Basin and the southern tier of states (Pearson et al. 2015). The maps of Wallis (1961) and Pearson et al. (2015) show *C. purpurea* occurring in Manitoba only in extreme southwestern Manitoba (Aweme, Brandon, Lyleton, Wawanesa). Lawton (2018) found *C. p. purpurea* in Manitoba's Interlake Region and north to Ponton, a remarkable northern range extension of 600 km. The author has also collected specimens in populations in southeastern Manitoba, so the species is now known to occur over much of southern Manitoba.

Habitat: The author has observed this species frequenting a variety of habitats such as meadow paths, grassy roadsides, gravel pits, and trails and clearings in mixed- and Jack Pine-forests, similar to what have been reported in other studies (Acciavatti et al. 1992, Graves 1963, Dunn 1981, Wilson and Brower 1983, Graves and Brzoska 1991). Criddle (1907) observed that in late September in Manitoba, these beetles sought out drier spots to hibernate, such as edges of sandy blow-outs, stubble fields, dry roadways and clay banks. In Alberta, Hilchie (1985) found it on patches of bare clay soil interspersed with clumps of grass and other plants. In the boreal forests of northern Manitoba, Lawton (2018) discovered it on seldom-used dirt roads, areas of human disturbance, bare soil in roadside ditches, and in open grassy areas under power-lines. While the author and other researchers have records of this species in prairie, parkland and boreal habitats in Manitoba, Acorn (2001) stated that this is strictly a prairie species in Alberta; "... found wherever grassy vegetation is having a tough time completely covering the ground."

Activity Period: A spring-fall species requiring two or three years for larval development; consequently both larvae (often third instar stage) and adults overwinter (Dunn 1981, Hilchie 1985, Pearson et al. 2015). Adults emerge from the pupal stage in late summer and early fall, hibernate during the winter, and then emerge in early spring to feed, mate and oviposit (Acciavatti et al. 1992). About 50 eggs are laid in May, singly, 7 to 9 mm into the soil, and two weeks later the larvae appear (Shelford 1908). Criddle (1907) observed that hibernacula descended 41-48 cm in sand, 15 cm in clay, and only 8 cm in a hard-packed roadside. Manitoba collection dates: March to September. Colleague Deanna Dodgson observed two individuals sunning on the sand at Mars Hill on 25 March 2021, with an ambient temperature of only 8°C. On March 20 the temperature had risen to a highly unusual 17°C, which appeared to have stimulated the beetles' emergence from hibernation. Acorn (2004) found an active individual on March 12, his earliest record for any tiger beetle in Alberta.

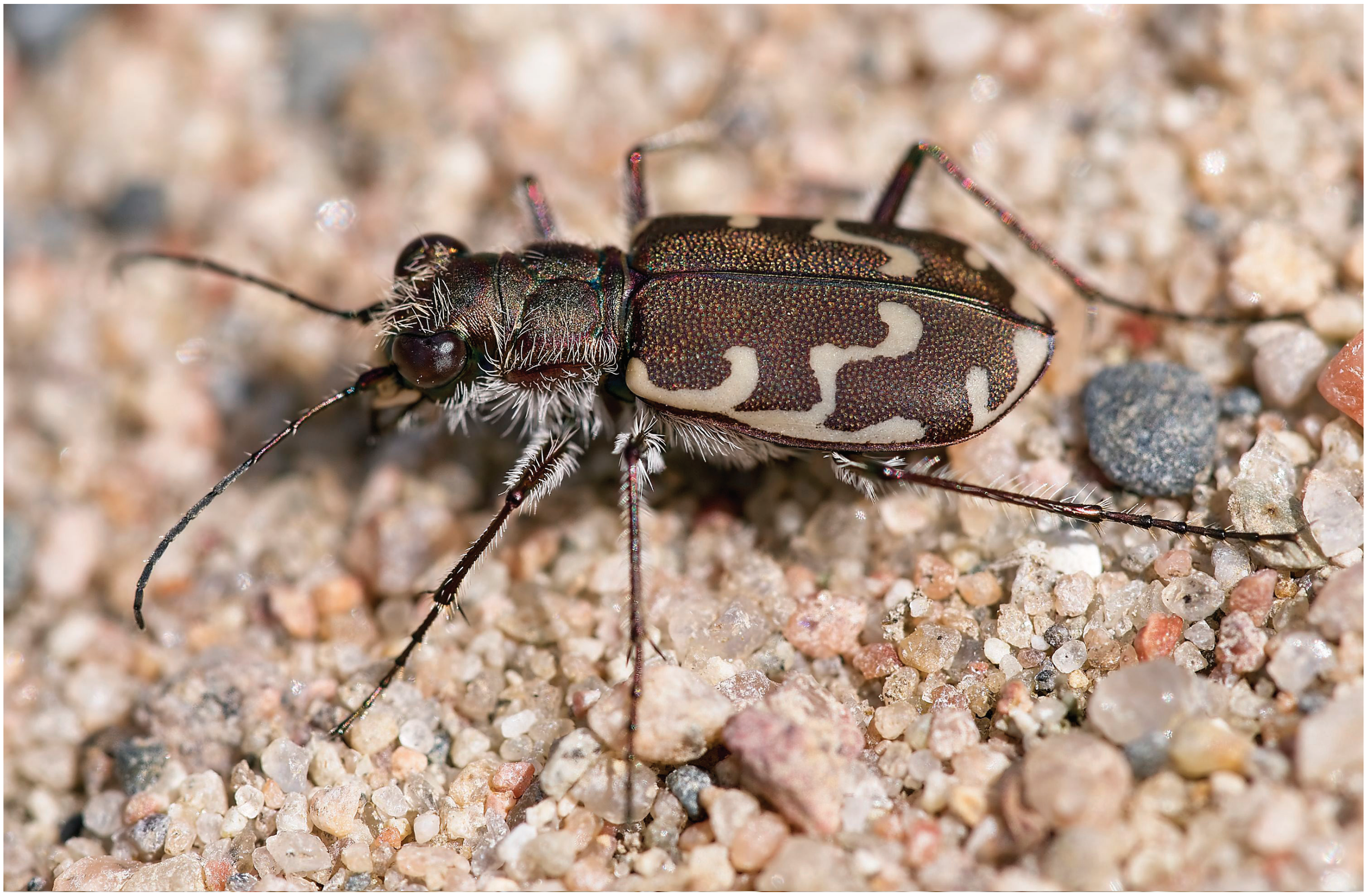
Remarks: This attractive species is found regularly in southern Manitoba, but apparently occurs sporadically in the north; it has not been found in the northwest of the province, but it is likely present there. Criddle (1907) noted that it is fond of sitting on the earth mounds of pocket gophers, whose dark soil and elevation offer additional heat and an unobstructed view of prey and predators. He further indicated that; "This insect is nowhere common, and is nearly always found singly or in pairs." Vaurie (1950) reported that in the mid-western states, this species is not gregarious, and Pearson et al. (2015) also pointed out it is usually found in low densities, which the author has also noted on many occasions. In fact, Leonard and Bell (1999) stated that this: "Harbinger of spring, *C. purpurea,* is not often collected [in Eastern Canada and New England]."

However, from 1995 to 2011, the author observed a consistently large population in an extensive glacial-till gravel pit beside the Julius Road, north of Highway 44, 3 km east of Seddons Corner. The surrounding forest consisted of Jack Pine, White Spruce, Paper Birch, Trembling Aspen and Balsam Poplar. In April and May of each year, the sparsely vegetated slopes (consisting of sand, gravel and some clay) and a compacted sandy path through the forest were inhabited by hundreds of recently emerged individuals, and sometimes over 40 (many copulating) could be observed at a time in a small area. *C. purpurea* overlapped in lower wet sites with abundant *Cicindela repanda*, and in higher, drier sites with *C. formosa* and *C. tranquebarica*. With recent resumption of gravel operations by heavy machinery, and consequent destruction of larvae in their burrows, population numbers of the beetles plummeted. When the author checked the surviving portion of the path in 2019, 2020 and 2021, it was still occupied by only a few *C. purpurea,* plus more-abundant *C. repanda*, *C.*

tranquebarica, and *C. longilabris*. With a possible future pause of gravel removal in the area, early plant succession and subsequent invasion of insect prey (such as colonies of ants) will likely enable the *C. purpurea* population to rebound. Surveying populations of tiger beetles over a number of years provides evidence of the ephemeral nature of many of their habitats due to natural causes (e.g., plant succession, erosion, flooding) and human disturbances (e.g., road ditches and gravel pits, which eventually become vegetated).

The term 'Cowpath' seems an inappropriate common name, since cowpaths are not a natural habitat, several other species routinely use cow trails, and the species inhabits other types of natural and disturbed habitats.

Conservation Status: Not officially rated; the Manitoba Conservation Data Centre listed this species as Unrankable. Recommendation: Secure.



(© Larry de March)

Bronzed Tiger Beetle (*Cicindela repanda* Dejean, 1825)

Description: The Bronzed Tiger Beetle is a small (11-13 mm), bronzy-brown species with a blue-green abdomen covered with setae. It has three complete maculations, mainly joined along the outer edge of the elytron, and with a 'C'-shaped humeral maculation (white shoulder mark). The apical lunule is not connected with the middle lunule.

Similar Species: This species closely resembles *C. duodecimguttata*, and there are some specimens that are not possible to determine using the extent of maculations alone. The thorax is square compared to trapezoidal in *C. duodecimguttata* (Leonard and Bell 1999). In *C. hirticollis*, the shoulder mark is clearly more 'G'-shaped rather than 'C' in *C. repanda.* Graves and Brzoska (1991) noted that in the field, *C. repanda* could be distinguished from other species by its shorter and more erratic flight, which was also noted by the author. Individuals often dart quickly just above the substrate and land only a metre or two away. It also averages slightly smaller than other shoreline species (i.e., *C. duodecimguttata* and *C. hirticollis*) with which it is commonly found.

Distribution: In Manitoba this species occurs throughout the lower half of the province, although there are few records north of Lake Winnipeg, mostly due to limited access for collectors. This is one of the most-widespread tiger beetles in North America, and in Canada is known from British Columbia to Labrador and Newfoundland. It is found throughout the United States except for most of the Great Basin, the Southwest, and southern Texas and Florida. Three subspecies are recognized, one of which, *Cicindela repanda repanda*, occurs in Manitoba (Pearson et al. 2015).

Habitat: The author found this species common to abundant on moist soil in ditches and along non-vegetated river banks and lake shores, especially mud flats and sandy bars close to the water's edge, as have other researchers (Wallis 1961, Hilchie 1985, King 1988, Graves and Brzoska 1991, Acciavatti et al. 1992). It is also common on moist sandy sites away from any water source such as trails, exhibiting a wider variety of habitat selection than *C. duodecimguttata* and *C. hirticollis* (Graves 1963 and personal observations). Criddle (1907) noted it as common in Manitoba along muddy roadways and wet fields, and also abundant along furrows and in wet spots in tall grain. Collin Hawkins (personal communication) collected it in many sites in southwestern Manitoba on sandy soil, mudflats, river banks, ditches, and lake shores. Willis (1967) lists habitats as both fluvial and non-fluvial, mesic and saline. Wilson and Brower (1983) noted it was rare or absent on gravel or rocky habitats. The larva burrows in moist, sandy soil (Graves and Brzoska 1991).

Activity Period: This is a spring-fall species, with a life cycle of two years, and with the third instar larva passing through the first winter, and the adult the second (Hamilton 1925, Hilchie 1985). Larval burrows descend about 50 cm in sandy sites, and only about 20 cm in clay (Criddle 1907). The old brood overlaps with the newly emerging adults by about ten days, the latter appearing from late July to early August in Manitoba. These hibernate over the winter, and are active and mate the following spring. While the usual time of emergence from hibernation in Manitoba is late April, soon after snowmelt, the author observed 4 specimens along the snow-free sandy shore of the Pembina River on 23 March 2012, a remarkably early date, but then that spring was unusually warm (even Leopard Frogs were active, but later froze). Manitoba collection dates: March to October.

Remarks: *Cicindela repanda* demonstrates the highest populations of any Manitoba species. On many occasions, the author has observed hundreds of individuals while walking along the wet edge of a sandy beach or muddy shoreline of a river. In such instances, abundant prey (such as flies and small ground beetles) can support large numbers of one or more species of tiger beetles (e.g., *Cicindela repanda, C. hirticollis* and *C. duodecimguttata*) (Pearson and Mury 1979, personal observations). Acorn (2001) reported a fascinating observation of an individual *C. repanda* jumping 20 cm into the air in an attempt to capture midges flying in a cloud. When tiger beetles are exceptionally abundant at a site, disturbed beetles seldom fly far, and the flight of one or more individuals causes many others to do the same, either by flying or running rapidly in all directions, which presents a significant distraction to a predator (and to the author!).

Larochelle (1977) cites a reference to this species being taken at a light during the night, but the author has not seen this.

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Unrankable. Recommendation: Secure

Bio-Fact: Male-guarding of a tiger beetle appears to be a compromise between preventing other males from displacing his sperm, versus forgoing mating opportunities with other females in the population.

(© Larry de March)

Festive Tiger Beetle (*Cicindela scutellaris* Say, 1823)

Description: The Festive Tiger Beetle is a robust, short-legged, small (11-14 mm) species characterized in Manitoba by its dull red, purple, brown, or green upper body, and with maculations reduced to the outside edges of the elytra. These may vary from a complete white line to reduced dots and triangles. Wallis (1961) recognized the form '*criddlei*' for western Manitoba specimens, with a broad, unbroken white band, and with Aweme, Manitoba as the type locality. The male is characterized by a white labrum and setose frons and vertex (front of the face), and the female by a black labrum and the loose cluster of setae near the front edge of each eye (Wallis 1961).

Similar Species: No other local species resemble *Cicindela scutellaris*.

Distribution: *Cicindela scutellaris* occurs from Alberta to Quebec and south through most of the central and eastern United States to New Mexico and Florida (Pearson et al. 2015). In Manitoba this species is found across the southern-most portions of the province. Among the seven subspecies currently recognized, the widespread *Cicindela scutellaris lecontei* occurs in Manitoba (Pearson et al. 2015)). Wallis (1961) considered the subspecies *Cicindela scutellaris criddlei* Casey, 1913, (named after entomologist Norman Criddle of Aweme, Manitoba) best regarded as a synonym of *C. scutellaris lecontei*.

Habitat: This beetle prefers dry, loose, light-coloured sand deposits, away from water (Graves 1963, 1965, Dunn 1981, Acciavatti et al. 1992). Sand dunes and sandy blowouts where vegetation is sparse provide ideal habitat (Wallis 1961, Acorn 2001, author's observations). Criddle (1907) and Collin Hawkins (personal communication) found it in dry sandy fields and at the edges of drifting sand among sparse vegetation. The author has also found it common to abundant in sand dunes with limited cover of vegetation, sandy road cuts in grassland, and along sandy trails in boreal coniferous forest. It often occurs with *C. formosa*, *C. lengi*, and *C. limbata* in dune fields. Interestingly, the author has never found individuals inhabiting the sandy shores of streams or ponds, where other species of tiger beetles abound.

Activity Period: This is a spring-fall species (Dunn 1981, Graves and Brzoska 1991) with a two-year life cycle, and with most individuals appearing from hibernation in May in Manitoba (author's observations). The second brood of adults emerges from August to September, then overwinters, followed by mating and oviposition (about 50 eggs) from April to May (Criddle 1907, Acorn 1991, Acciavatti et al. 1992). Consequently, this subspecies hibernates both as adults and larvae (Acorn 1991, Hilchie 1985). Larval burrows range in depth from 25 to 80 cm in stabilized sand, often with a side pupal chamber (Shelford 1908). The beetles begin to go into hibernation relatively early, in September, and then emerge in April, either early or late, depending on weather conditions and snow cover (Criddle 1907). Manitoba collection dates: April to October.

Remarks: The species name *scutellaris* may refer to the rectangular, shield-like (Latin *scutulum* -- an oblong shield), coloured area of the elytra. The author has come across abundant *C. scutellaris* along a sandy trail in prairie in the Carberry Sandhills, and a sandy trail through Jack Pine forest near the Sandilands Forest Discovery Centre, south of Hadashville. At times, while hiking along these trails, literally dozens of individuals could be seen, taking off and flying a short distance ahead. If 'pushed' repeatedly along the trail, they usually fly into adjacent vegetation and are lost from view.

This species has the habit of 'freezing' in place once it is covered by a net, making it challenging for the collector to locate it. Once the rim of the net is lifted even slightly for a look, the beetle escapes with astonishing speed – an ability also noted by Criddle (1915). This provides evidence of the beetle's excellent eyesight in rapidly determining an escape route (possible by contrasting light levels).

Larvae in their burrows may be subject to high rates of attack by parasitoid species of the bee-fly *Anthrax* (Pearson et al. 2015).

The construction and maintenance of the burrow, over many months or years by a growing tiger beetle larva, are energetically costly, which is likely the reason larvae are so reluctant to leave their burrow in search of a site with improved prey opportunities. Consequently, larvae are seldom found on the surface. Perhaps they reduce their metabolic rate while inside the burrow so as to tolerate famine, even if death ensues. However, flooding and drought have been found to force burrow abandonment and search for a more suitable site.

Pearson et al. (2015) stated that; "This species shows the greatest geographical variation among populations of any tiger beetle species in North America, and exhibits colors ranging from maroon and bright metallic orange to blue, green, and black." Graves and Brzoska (1991) suggested that *C. scutellaris* is so highly polytypic, a thorough study of geographic variation is required. In fact, this species varies so markedly in colour and morphology that some taxonomists view certain subspecies are on the verge of becoming full species. However, Pearson and Vogler (2001) stated; "But it is not clear whether these obvious differences in coloration and body size indeed reflect deep evolutionary differentiation."

Shelford (1908) noted that captive individuals underwent a series of colour changes from freshly emerged to death.

The author has in his collection specimens of several different-looking subspecies, such as the beautifully multicoloured *C.s. yampae* of Colorado, and the bright, completely blue *C.s. unicolor* from Florida. One would never conclude at first glance that they could possibly be the same species.

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Unrankable. Recommendation: Secure.

(© Larry de March)

Oblique-lined Tiger Beetle (*Cicindela tranquebarica* Herbst, 1806)

Description: This is a medium-sized (11-16 mm) tiger beetle with oblique humeral maculations, and variable within and among populations. Generally dark brown, individuals may be black or bronze, with a green, coppery or black abdomen. *C. tranquebarica kirbyi* is typically brown or bronze above with wide white markings, and is dominant in the prairie and boreal regions of Manitoba. This subspecies intergrades with *C. t. tranquebarica* in southeastern Manitoba, which is dark brown with slender maculations (Pearson et al. 2015).

Similar Species: The Oblique-lined Tiger Beetle is distinguished from others by its distinctive white shoulder mark, which is straight and angled inwards and backwards, toward the elytral midline. *Cicindela formosa* is larger, with a short, curved shoulder mark, and broader maculations. *Cicindela lengi* is noticeably slimmer, reddish, and has light markings over 50% of the elytra.

Distribution: This common tiger beetle is one of the most-widespread species in North America, occurring from British Columbia and the Northwest Territories to Newfoundland, and through most of the United States, except for the Pacific coast and the deep South (Pearson et al. 2015). It is found in the lower two thirds of Manitoba, with the northern record at Stephens Lake, near Gillam (Lawton 2018).

Habitat: The author has found *C. tranquebarica* present in almost any tiger beetle habitat, ranging from open areas in mixed-grass prairie, boreal-forest trails, wet and dry alkaline mud flats, sandy blowouts, gravel pits, and open wet patches along roadside ditches. Criddle (1907) also found it on open sites in numerous localities – "Dry land and wet land, sand, mud or alkali seem to be alike suitable to its tastes." Disturbed sites appear to be colonized rapidly.

Activity Period: This is a spring-fall species, however midsummer stragglers are common (Dunn 1981). The life cycle covers two or more years. Hibernacula descend from 28-61 cm in moist or dry sand or clay (Criddle 1907). Adult beetles emerge from pupation in late summer and early autumn, hibernate, and are active the following spring (as soon as the the ground thaws) with subsequent mating and egg laying (Criddle 1907, Acciavatti et al. 1992). Overwintering occurs as larvae and adults (Hilchie 1985). Manitoba collection dates: April to October.

Remarks: This species demonstrates wide variation in colour (green to almost black) and pattern over its large range, and over two-dozen subspecies have been described in the past, many of which are now considered invalid (13 are recognized provisionally by Pearson et al. 2018). Acorn (2001) made the interesting observation that; "Greenishness shows up in many sorts of tiger beetles at the edges of the species' range, typically in high altitudes or northern locations. This makes many tiger-beetlers suspect that the environment, not genetics, causes some types of green colour." In fact, Shelford (1917) demonstrated in laboratory experiments that dorsal colour is partly determined by developmental conditions during pupation. With mammals (e.g., black Grey Squirrels and black Plains and Northern pocket gophers), peripheral populations may also demonstrate different pelage colour, and researchers usually conclude that genetic drift in semi-reproductively isolated populations is the cause, and not environmental selective influences.

This species' burrows are often present in high densities and are heavily attacked by the parasitoid bee-fly *Anthrax*. Schultz and Hadley (1987) observed specimens in a northern Arizona stream-side shuttling between sunny and shaded upper-beach sites as air temperatures rose above 35°C. Under laboratory conditions, they determined a lethal temperature of 46°C.

Often occurring singly or in small numbers, on occasion the author has come across really abundant populations. Since numbers can vary considerably from year-to-year, and seasonally, one can never view a suitable habitat and know beforehand how many individuals will be present. The anticipation of finding a species contributes to the excitement of searching for tiger beetles in general.

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Unrankable. Recommendation: Secure.

Suggestion: "The easiest way to get a good photograph is to catch a beetle in a net, then place it in a small bottle and put it in the cooler overnight. It can be photographed during that cool period in the early morning with blue sky providing optimal lighting. Habitat can be recreated in a cereal bowl (which can be later used for breakfast). When first removed from the bottle it will be slow and there will be a brief opportunity for a good photograph." (Catlin PM. 2006. Tiger beetles (*Cicindelidae*) of the Northwest Territories: distribution, status and other information.)

(© Larry de March)

Punctured Tiger Beetle (*Cicindelidia punctulata* Olivier, 1790)

Description: This small (10-13 mm), brownish-black, and narrow-bodied tiger beetle may be identified by a row of metallic blue/green punctures (hence the species' name) on each elytrum, near the midline; however, these are only apparent with a specimen in hand or under magnification. White maculations may be absent or reduced to small spots and thin lines.

Similar Species: *Parvindela terricola* is similar to *C. punctulata*, but the former lacks the two rows of elytral punctures, is blacker, and usually has more prominent maculations on the outer elytral edges.

Distribution: This species has a broad range from Alberta to Quebec and south to California, Arizona, Florida, and Mexico (Cazier 1954, Pearson et al. 2015, Richardson and Johnson 2019). In Manitoba, it occurs only in the extreme south, more often in the west than the east. Lawton (2018) extended the range 130 km north with a specimen taken at St. Laurent; possibly the species has spread northward to this site in recent times by following saline patches that have developed recently in roadside ditches along Highway 6.

Habitat: *Cicindelidia punctulata* is observed sparingly on sparsely vegetated substrates, such as sandy loam on paths and unpaved roads, and on dry prairie with open patches between the grass clumps (author's observations, Wallis 1961, Graves 1963, Hilchie 1985). It does not enter open sand dunes or beaches in Manitoba, but the author found it regularly on the edges of watercourses and lakes in the western United States (a beautiful blue-green subspecies

C.p. chihuahuae). Willis (1967) described its habitat as nonfluvial (not relating to a stream or river), mesic, and saline habitats, although sometimes fluvial. Criddle (1907) located it at only few sites in the Carberry Sandhills (Aweme), where on occasion it was common. The author found a few specimens almost annually along the sandy trails leading to the Bald Head Hills in the Spruce Woods Provincial Park, but it was never common. Collin Hawkins (personal communication) recorded specimens in roadside ditches with sparse grass in western Manitoba.

Activity Period: This is a summer species with adults appearing in July and most dying off by the end of August (Criddle 1907, Dunn 1981, Graves and Brzoska 1991, author's observations). It overwinters in the larval stage and requires one, and under some conditions, two years to reach maturity (Wallis 1967, Hilchie 1985). Eggs are laid in late July and hatch in two weeks. The first and second larval stage each last for three weeks, and the third is generally reached by September. After hibernation, the larva feeds from May to early June, then pupates and emerges in July (Shelford 1908). The burrows have been found to descend to a depth of 14-66 cm (Criddle 1907, Pearson et al. 2015), rather amazing for such a small tiger beetle. Some burrows feature a side pocket where the pupal stage is passed (Shelford 1908). Manitoba collection dates: July to October.

Remarks: This may be the most-abundant tiger beetle in North America (Dunn 1981, personal observation). The author has even found it frequently within towns, with numerous observations of multiple individuals at night on sidewalks, lawns, and especially under night lighting at gas stations and car washes. At the northern edge of its range in southern Manitoba, it is one of the rarer species of tiger beetles. When disturbed, it often prefers to run into nearby cover, however it is a rapid flyer, seldom straying off or along the path for more than a couple of metres. It seems to vanish in flight due to its small size, and on landing, its black colouration offers perfect camouflage among pieces of dark plant debris and vegetation.

Like most species of diurnal tiger beetles, on hot days this species first begins to 'stilt' high up on its long legs above hot substrates, and as the mid-day heat builds up to over 34°C, it seeks refuge by shuttling into shady sites under vegetation. At 38°C, it hides under mud cracks or digs out and remains hidden in a shallow burrow.

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Not Recorded. Recommendation: Secure. Although not recorded at many sites in the province, it is locally common in the Spruce Woods Provincial Park, and consequently this particular population is secure. Populations outside the park, inhabiting roadside ditches, would be subject to periodic flooding, chemical spraying for weed control, and being crowded out by plant succession.

Bio-Fact: A diurnal tiger beetle runs so rapidly when hunting and pursuing moving prey that its eyes are unable to capture sufficient photons to sense prey movements and direction, so it must stop for an instant in between successive dashes to finally home in on its prey. The antennae, held stiffly in a forward position (bent down at the ends) only millimetres above the substrate, provide continual contact information (i.e., 'mechanosensation') on obstacles, permitting instantaneous avoidance of plant stems and uneven ground surfaces (Zurek and Gilbert 2014).

(© Stephen Spomer)

Coppery Tiger Beetle (*Ellipsoptera cuprascens* LeConte, 1852)

Description: The Coppery Tiger Beetle is a medium-sized (10-14 mm) tiger beetle with full markings that vary from coppery red to green. Willis (1967) found that northern populations in the central United States are greenish, which will likely be the case if additional specimens are collected in Manitoba. The front or humeral maculation is 'G' shaped (not 'J') pointing to a prominent white dot on the shoulder. A thin white line on the outer edges of the elytra connect all three maculations. The elytra are shiny and deeply punctate (i.e., studded with tiny pits).

Similar Species: *Ellipsoptera cuprascens* is similar to *E. nevadica,* but the prominent white dot at the top of the 'G' in the humeral area distinguishes the former species.

Distribution: This species is known in Canada only from a single site in southwestern Manitoba, with only a few specimens taken over half a century ago in the Spruce Woods Provincial Park (noted by Wallis 1961 as 26 km east of Aweme). It is an abundant and widespread species throughout the central United States, as far south as New Mexico, Alabama, and West Virginia (Pearson et al. 2015).

Habitat: Adults are associated with damp sandy or muddy shorelines and flats along rivers and streams during the early summer months (Acciavatti et al. 1992, Graves and Brzoska 1991). Willis (1967) reported it from fluvial, mesic and saline habitats. The author has collected numerous specimens along the sandy shores of many rivers in the central United States.

Activity Period: This is a summer species which emerges in June and attains peak activity in July and August (Graves and Brzoska 1991, Acciavatti, et al 1992). It has a two-year life cycle. Larvae are capable of moving to a new site if their burrow becomes too dry or hot (Larochelle and Lariviere 2001). Manitoba collection dates are unknown, but were probably June and July, as occurs in the northern United States.

Remarks: Wallis (1961) reported that occasional *Ellipsoptera cuprascens* specimens were captured at intervals over several years at a sandhill-spring site locally known as the Punch Bowl in Spruce Woods Provincial Park. He further stated that; “Search for this species along the river [Assiniboine] and in other apparently suitable situations has been unavailing. Perhaps, then, this species is not a permanent resident at this site, but only an occasional visitor.”

The ‘Punch Bowl’ in the Carberry Sandhills – the former site of the only-known population of *Ellipsoptera cuprascens* in Manitoba. (© Robert Wrigley)

Over the past three decades, the author and others have failed to find this species at the original site, and other species (*Cicindela formosa* and *Cicindela repanda*) were occupying the sandy slopes that surround the pond. This landscape feature is only a short distance from the sandy shoreline of the Assiniboine River, and these extensive exposed sand flats (subject to flooding and reforming), being typical habitat for this species, was likely the initial source of the Punch Bowl specimens. It is certainly possible that a population still survives along the hundreds of kilometres of the river, however the nearest currently known population lies over 200 kilometres to the south in North Dakota, so there would seem to be only a slight possibility of new immigration.

Larochelle (1977) and Pearson et al. (2015) noted that this species was attracted to lights. As opposed to the similar-looking *Ellipsoptera nevadica, Ellipsoptera cuprascens* is not usually a gregarious species (Pearson et al. 2015. However, on the night of 23 July 2003, along a sandy shore of the Red River south of Foreman, Arkansas, the author was surrounded by many hundreds of *E. cuprascens* attracted to his headlamp and flashlight. The beetles appeared dazed by the light and dashed back and forth, repeatedly, at great speed, running rapidly, pausing, and then flying off for about a metre. Numerous individuals landed on him and then promptly took off. While stationary, they were easily captured by hand. On another trip to the same site a few years later, the shore and riparian forest were completely flooded for many weeks, destroying untold numbers of tiger beetle larvae as well as adults, which had access to no other suitable habitat in the region. Likely numbers recuperated over the next couple of years as the river returned to normal levels and the beetle's sandy beach habitat reappeared. It was a remarkably demonstration of how high water and fast current can temporarily sweep away not only suitable habitat for tiger beetles, but also invading grasses and sandbar willows, thereby generating periodically new quality habitat of barren sandy shoreline for tiger beetles.

This species demonstrates an interesting case of sexual dimorphism in that the mandibles are significantly longer and curved, and the labrum (upper lip) is shorter, in the male, modifications presumably to assist the male in grasping and holding onto the female (at the indentations in front of the elytra known as 'coupling sulci') during mating (Pearson and Vogler 2001). These differences are well illustrated in photographs by Ted MacRae (2012)

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Imperiled. Recommendation: Extirpated.

(© Larry de March)

Ghost Tiger Beetle (*Ellipsoptera lepida* Dejean, 1831)

Distribution: Due to its specific habitat requirement of fine bare sand, this species has a remarkable discontinuous distribution from southeastern British Columbia to southern Quebec, and south to Arizona, Texas, Louisiana, and Mexico (Pearson et al. 2015). Its only occurrence in Manitoba is in the active dune area of the Carberry Sandhills.

Description: This is a small (8-12 mm), pale tiger beetle, with a few obscure, green to brown pale markings on the elytra, and with gold highlights on the reddish-bronze or green pronotum. All but the elytra are densely covered with flattened white setae, including the pale legs. Shelford (1917) noted that when the pigmented elytral markings begin to develop, they are a brilliant gold for several days, and then darken to light brown.

Similar Species: *Cicindela limbata* occurs in the same habitat as *E. lepida,* and is also small and pale, but the legs are dark and the elytra have more prominent and darker-brown maculations than in the former beetle. *C. limbata* is alert, flighty, and flies off for several metres, while *E. lepida* runs or flies only a metre or two.

Habitat: This is a species of barren sand dunes, and is now restricted in the Carberry Sandhills to a few areas of sand flats and bowls of dunes. This is typical habitat for the species reported by many other studies – on fine, pure white or pale yellow sand, away from vegetation (Graves 1963, Hilchie 1985, King 1988, Wallis 1961). Criddle (1907) first reported it in Manitoba's Carberry Sandhills on drifting sand plains, usually on the sunny, wind-blown side of a sand bank. King (1988) did not find it on apparently suitable habitats of pure white sand more than 5 metres from water, however most other authors have observed this species at great distances from any water source. This species' habitat of barren sand dunes overlaps with that *Cicindela limbata, C. formosa,* and *C. scutellaris,* with these three species preferring to remain close to sparse vegetation.

Activity Period: A summer species, this beetle emerges from the pupal stage from late June to early July, and dies out before the end of August. Mating may occur inside the burrow. Two years are required to complete the life cycle, with only the larval stages in hibernation, and the adult stage lasting for less than a month (Shelford 1908, Criddle 1907 and 1910, Hamilton 1925, Acorn 1991, Brust et al. 2005). Larvae occur in sites of shifting sand in burrows that are up to 180 cm deep (Hamilton 1925, Brust et al. 2005) – a remarkable depth for such a tiny and delicate insect. In late September in Manitoba, Criddle (1910) uncovered first-year larvae in burrows 23-28 cm deep (81 cm deep in soft sand), and larger second-year larvae down to 184 cm. In describing the habitat of barren dunes in Manitoba, Criddle (1910) stated; "The larval holes...are right on the drifting sand and one wonders how the insects manage to keep their holes open or procure sufficient food in such a desert. As a matter of fact there is evidence to indicate that such unfavorable conditions have at least lengthened the larval life to a year beyond the average." While barren sand dunes support limited prey resources compared to vegetated sites, the small size of both the larva and adult Ghost Tiger Beetle would require less nutrition to complete the life cycle, compared to the large Big Sand Tiger Beetle.

Most Manitoba specimens the author and a few other researchers have collected were taken in July. Individuals reportedly become inactive when the surface temperature exceeds 48°C (Hilchie 1985), but the author's observations in southern Manitoba indicate that individuals seek shelter well below this high ambient temperature, in the mid-to-high 30°s C. The sand temperature of course would be significantly higher. On a warm afternoon in July, when surface activity had ceased, the author was able to scoop out by hand specimens that had excavated shallow burrows (the blocked entrance marked by a tiny crescent) on a low-sloping sand dune. The species remains active on warm nights (Acorn 1991). Manitoba collection dates are from June to August.

Remarks: This beetle is justifiably referred to as the Ghost Tiger Beetle due to its cryptic colouration, which closely matches that of light sand. Only naturalists who choose to look for it in the month of July in the Carberry Sandhills would ever have a chance to find it, and it would easily be missed without knowing where and what to look for. In fact, *E. lepida* is seldom detected even at close range until it moves, and then one usually must try to follow its faint shadow to keep track of its running course, or short, low flight. When it stops running or lands, it seems to vanish, and only its shape and slight shadow sometimes give away its location.

Criddle (1907) found this species plentiful only once during decades of study in the Carberry Sandhills. Preston noted it as very abundant in early July, 1997, although he had never observed it there on numerous previous visits. The author found it in low numbers over the years, and abundant only twice -- on 7 July, 1999, and 9 July, 2006, about 60 were observed at two favoured sites in early afternoon. In many other years it was rare or absent. Acorn (1991) captured an astonishing 606 specimens from June 30 to August 9, 1984 (peaking close to 300 during the week of July 12-19) in pitfall-traps in the Empress Dunes south of Empress, Alberta. It would be interesting to know what factors promote these occasional peaks in abundance, although some peaks would be missed due to lack of observers during the short active period of adults.

Another possible explanation for its scarcity of observations during the day may be its preference for night activity. The author has experienced this trait with two other species – the White-striped Tiger Beetle (*Parvindela lemniscata*) in southern Arizona, and the Coppery Tiger Beetle (*Ellipsoptera cuprascens*) in Arkansas. In each case, many hundreds arrived at his mercury vapour light, while during the day, none or a few dozen were seen. Vaurie (1950) also remarked on the nocturnal activity of this species; "Although seen occasionally in the daytime, *lepida* was always more abundant at dusk or after dark, at which time it was taken by hand in the light of a lantern." Larochelle (1977) cites nine references to this species being taken at night lights. Hilchie (1985) collected flying adults in a light trap many kilometers from the nearest dune. This is a remarkable event considering the species' small size and it being the weakest flier among Manitoba tiger beetles (Criddle 1907, personal observation). Graves and Brzoska (1991) also noted that adults fly only a short distance when disturbed. On 8 July, 1997, Preston found one individual in the mandibles of an immature lycosid spider, probably *Geolycosa wrightii*, a common species in the area.

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre listed this species as Critically Imperilled. Recommendation: Endangered. This designation is due to it being found in only a few areas of bare sand in the Bald Head Hills of the Spruce Woods Provincial Park.

While a member of the Manitoba Endangered Species Advisory Committee in the 1990s, the author recommended this species be rated as endangered due to its single occurrence in the province, and to the fact that most of its former, extensive habitat of barren dunes had been lost by succession to grassland and spruce-oak-poplar forest over the centuries, a process that continues to this day. He further recommended mechanical removal of vegetation and prescribed fire to prevent further encroachment of vegetation onto the active dunes, practices that have been recommended in other conservation assessments for this species (Panella 2012).

An eastern section of the Carberry Sandhills was formerly part of the Canadian Forces Base Shilo, and so was off limits to the public. The area was subjected to bombing, tank traffic, and frequent fires until 1975 when it was added to the Spruce Woods Provincial Park. Soon after, the open sand dunes became over-run by all-terrain vehicles until they were banned from the Park. The limited locations where the species has been observed over the years are along designated hiking trails, so foot traffic may destroy some beetle larvae. However, this use is unlikely to have any long-term destructive effect on the beetles or their habitat. Fortunately, this small population in Manitoba currently gains protection by being located in the Spruce Woods Provincial Park.

Pearson et al. (2015) stated the species is; "Now absent from many of its historical breeding sites [throughout Canada and the United States], probably due to sand excavation, land development and stabilization of sand dunes by encroaching vegetation." It may be that off-road vehicle and foot traffic are also threats. The species is considered threatened in nearby Minnesota (Coffin and Pfannmuller 1988), and variously rated as vulnerable, threatened, imperiled, critically endangered, or extirpated in over a dozen states and provinces (explorer.natureserve.org/servlet/NatureServe).

This barren sand valley between the dunes in the Carberry Sandhills is surprisingly the preferred habitat of the Ghost Tiger Beetle. The beetle is so small and well camouflaged that most passersby would fail to notice it. The partially vegetated borders host both the Sandy Tiger Beetle (sometimes straying out into the open) and the Big Sand Tiger Beetle. (© Larry de March)

(© Stephen Spomer)

Nevada Tiger Beetle (*Ellipsoptera nevadica* LeConte, 1875)

Distribution: *Ellipsoptera nevadica* occurs from southeastern Alberta to extreme southwestern Manitoba, and south through the central United States, with isolated populations in California, Arizona, New Mexico, Texas, and Mexico (Willis 1967, Pearson et al. 2015). The only known Manitoba records are from the "shore of Watsons Lake, about 6 miles south of Hilton," taken in 1957 (Wallis 1961). The lake site is actually situated at 6.6 km SSW of Hilton. Another researcher (Willis 1967, map p. 277) shows an additional, unspecified locality record for this species in the Spruce Woods area, but this is a misinterpretation of Wallis' map on page 66.

Description: This is a medium-sized (10-13 mm) species, shiny green or reddish brown, and with three full maculations connected by white on the outer elytral edges. The humeral maculation is sharply 'J' shaped (not 'G'). The setae lie flat on the body rather than being erect. Among eight subspecies, Pearson et al. (2015) listed *Ellipsoptera nevadica knausii* Leng, 1902, as occurring in Manitoba.

Similar Species: This species closely resembles *Ellipsoptera cuprascens,* and may be distinguished by the latter's prominent white dot in the humeral (shoulder) region. *C. hirticollis* is slightly larger, has tufts of erect white seta on the sides of the thorax, and selects freshwater sites (i.e., not salt flats).

Habitat: *Ellipsoptera nevadica* occurs on wet sand and mud along ditches and sparsely vegetated borders of saline or alkaline streams, creeks and lakes (Vaurie 1950, Wallis 1961, Willis 1967, Hilchie 1985, Pearson et al. 2015).

Activity Period: This is a summer-active species, June to August in southern Canada, with over-wintering larvae (Acorn 2001). The female lays 2-mm-long eggs in soil with a high salt content, which helps avoid larval competition with those of other species. With a two-year life cycle, the larvae may spend over 11 months underground, and about six weeks as an adult on the surface (US Fish and Wildlife Service, Endangered Species Report). The third instar larva is 18-20 mm long. Criddle (1907) and Shelford (1908) noted that the larvae of all species studied pass through at least one winter. With the approach of cold weather (late September) they dig their burrows deeper, piling the sand beside the opening in a single heap. They finally stop digging and close the mouth of the burrow with soil, go to the bottom, and remain there until spring. Burrows in this species descend to 18-35 cm (Willis 1967). The only Manitoba collection dates are 19 to 20 July, 1957.

Remarks: Willis (1967) examined 10 males and 10 females from the single locality at Watsons Lake in his study of tiger beetles of saline habitats. Consequently, the presence of this species in Manitoba was not the result of a single wayward individual, but of a once-viable population. Preston and others investigated the Watsons Lake area, but did not find the species in the badly overgrazed habitat. While the species may still exist in small numbers elsewhere in extreme southern Manitoba, it has not been seen since 1957. With the region highly modified by agriculture for well-over a century, it is likely the species has been extirpated in the province.

Willis (1967) surmised that *Ellipsoptera nevadica* evolved in the western United States and became widespread during the early Pleistocene pluvial periods, when moist climates permitted easy dispersal. During the drier interglacials, many populations were apparently extinguished, resulting in isolation and the development of geographic races. During the Wisconsinan glaciation, *E. nevadica knausii* was forced as far south as Texas, and with the final retreat of the glacier, it rapidly spread north to the Dakotas and southern Canada.

The author's observations in the United States, and those of others (e.g., Larochelle 1977, Pearson et al. 2015), have revealed that the species is also active at night. It is usually more gregarious than its look-alike *Ellipsoptera cuprascens.*

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre lists this species as Unrankable. Recommendation: Extirpated.

The subspecies *Ellipsoptera nevadica lincolniana*, known as the Salt Creek Tiger Beetle, confined to saline wetlands in Nebraska, is listed as Endangered under the U.S. Endangered Species Act due to over 90% loss of its wetland habitat from farming and other human developments. With less than an estimated 1000 surviving individuals, a number of organizations including zoos are attempting an experimental reintroduction and a habitat-monitoring program (Palmer and Klatt 2014).

Bio-Fact: In regards to nocturnal activity of tiger beetles, Vaurie (1950) found 26 species active at night, including *Cicindela repanda, C. limbata, Ellipsoptera cuprascens, E. nevadica, E. lepida,* and *Cicindelidia punctulata,* while strickly diurnal species were *Cicindela formosa, C. fulgida, C. hirticollis, C. lengi, C. purpurea* and *C. scutellaris.*

(© Larry de March)

Variable Tiger Beetle (*Parvindela terricola* Say, 1824)

Description: At 8-10 mm, this is one of the province's smaller tiger beetles. Two subspecies are recognized in this region – *P. t. terricola,* which is black, blue or dark brown dorsally with maculations absent, and *P. t. cinctipennis,* which is brown, brownish-green, green, or blue dorsally, with complete maculations that are joined along the edge of the elytra (Pearson et al. 2015). The abdomen is dull black in *P. t. terricola* and bright metallic green in *P. t. cinctipennis*. Populations are highly variable in Manitoba, and in all areas there is a blend of *terricola* and *cinctipennis* characteristics. Consequently it is not possible to assign subspecific designations. Pearson et al (2015) concluded that; "Numerous attempts to make taxonomic sense of this group using classic adult characters as well as molecular DNA have yet to be successful." Ronald Huber (personal communication) is of the opinion that the formerly recognized species *Cicindela pusilla* (now a synonym of *P. terricola*) should be resurrected as a distinct species *Parvindela pusilla*.

Similar Species: Black or bronze specimens of *Parvindela terricola* look like *Cicindelidia punctulata,* but the latter has a row of punctures (which are barely visible without magnification) along each side of the elytral suture.

Distribution: This species occurs in southern Canada from British Columbia to northwestern Ontario, with isolated populations in Peace River, Alberta and southern Yukon, and in the United States, south to Minnesota, California and New Mexico (Wallis 1961, Pearson et al. 2015). It is present in low numbers in sparse mixed-grass prairie in southern Manitoba. The author found five specimens a few kilometres north of St. Laurent on June 25, 2000, and Lawton (2018) found specimens farther north in the Interlake at 11 km south of Fairford.

Habitat: This beetle occurs sporadically on bare saline soils, now usually along roadside ditches in Manitoba. Likely most of its original mixed-grass pririe habitat in agricultural regions of the province have been eliminated. Summarizing the observations of many researchers, Pearson et al. (2015) stated that this species inhabits; “open grassy ground that is muddy or dry, but usually alkaline or salty...in grassy areas of dry creek beds, salt lakes, irrigation ditches, banks and bars of rivers, sage brush areas, and shaded paths in open forests.”

Vaurie (1950) also noted that this species was not gregarious, and its main requirement was grass or low plants alternating with small open spaces in alkali situations.

Activity Period: This a summer species, with Manitoba collection dates in June, July and August. In Alberta, Acorn (2001) also reported emergence of adults in June, reproducing in July, and dying out in August. Populations in the southern part of the range have a one-year life cycle, and are active from April to September (Pearson et al. 2015), although the life span of individuals in Manitoba may extend to two years. Little is known about larval stages. Burrows have been reported in bare patches of clay soils.

Remarks: The author found five specimens of *Parvindela terricola*, among over 100 *Cicindela westbournei*, on saline flats a few kilometres north of St. Laurent on 25 June, 2000. Pearson et al (2015) and the author’s observations indicate that *Parvindela terricola* is usually solitary, or occurs in small numbers. However, on 1 July, 1997, Colin Hawkins took the author collecting for tiger beetles along Highway 24, between Rapid City and Oak River, and numerous bare, saline patches along the grassy roadside ditch supported large numbers. Most individuals ran or flew for only a metre or two when disturbed, and we could have easily captured a hundred specimens. During occasional summers, this species was common in saline patches along the Perimeter Highway north of Winnipeg, however in most years, it appeared to be absent. It is the nature of some tiger beetle species and populations to fluctuate in abundance over the years.

Conservation Status: Not officially reviewed; the Manitoba Conservation Data Centre lists this species as Not Ranked. Recommendation: Secure.

TIGER BEETLES AS MODELS

Logo of the Young Entomologists (Entomological Society of Manitoba), depicting *Cicindela formosa manitoba*, and created by Carol Galloway in 1981 (left). The image was modified by Ms Galloway and adapted for the Entomological Society of Manitoba in 1992 for Volume 48 of the Society’s Proceedings. It remains the Society’s logo to this day (middle). The Joint Annual Meeting of the Entomological Society of Canada and the Entomological Society of Manitoba, held in Winnipeg in 2017, also used a logo with *Cicindela formosa*, prepared by Aldo Rios Martinez (right). (© Jordan Bannerman)

Tiger beetle and its lady-beetle prey. Welded and painted steel. Colin Hawkins of Rapid City, Manitoba. The late Colin Hawkins used his welding talent to create a variety of insects from scrap metal and machine parts. The lady beetle was a halved ball-cap from a gas cylinder. Colin focused on collecting tiger beetles and hawkmoths, and traded insect specimens worldwide, especially with colleagues in France and Japan. His tiger beetle collection is currently with the author, who will eventually direct it to the JB Wallis/RE Roughley Museum of Entomology. (© Robert Wrigley)

Bronze models of the Great Plains Giant Tiger Beetle (*Amblycheila cylindriformis*) (model length 145 mm) and the Giant African Manticore Tiger Beetle (*Manticora latipennis*) (170 mm). Bronze casts using the lost-wax method by the author's sculptor-friend George Foster of Quebec. The author sent George a dried specimen of *Amblycheila* which he collected south of Hot Springs, South Dakota. The *Manticora* specimen was acquired through purchase. (© Robert Wrigley)

The author acquired an accurately cast bronze ‘formosa’ tiger-beetle belt buckle manufactured by SilverspotStudio. Owner Jessee Smith informed him that two famous entomologists from Canada had also purchased it – Alberta cicindelophiles the late Dr. George Ball, and Dr. John Acorn, who kindly provided the photo.

The author’s tiger beetle belt buckle. (© Arlene Dahl)

THE ASTONISHING WORLD OF TIGER BEETLE MICRO-SCULPTURE

The following marvelous series of Scanning Electron Microscopy (SEM) images was taken by cell biologist Dr. Erwin Huebner at the University of Manitoba. As both Professor Emeritus in the Department of Biological Sciences, and Artist in Residence in the School of Art, he integrates the worlds of microscopic life and art. The author was invited to spend an exciting morning in Erwin's lab to observe his remarkable scanning technique utilizing several species of tiger beetles.

"One long fascination has been exploring the incredible imagery of the microscopic world. As Victor Hugo once said "Which gives a grander view – the microscope or the telescope?" For me it's the microscope. Having knowledge of the many facets of optics, tissue and material properties, an entire new artists' palette has emerged for me. Using the microscope as an 'artist's brush' and the slides and imaging as a canvas, it has been, and continues to be, a wondrous journey of excitement and imagination.

"One focus of exploring microcosms has been highlighting the beauty and intriguing structures in microscopic worlds that are hidden from the naked eye. The imagery depends on interactions of natural materials with light, electrons, and one's imagination. Some of my books illustrate 'micro-landscapes' and exploration of textures, colors, incredible micro-architecture of living organisms and patterns within patterns." Dr. Erwin Huebner.

Dr. Erwin Huebner preparing to take images of tiger beetles with his scanning electron microscope at the University of Manitoba.
(© Robert Wrigley)

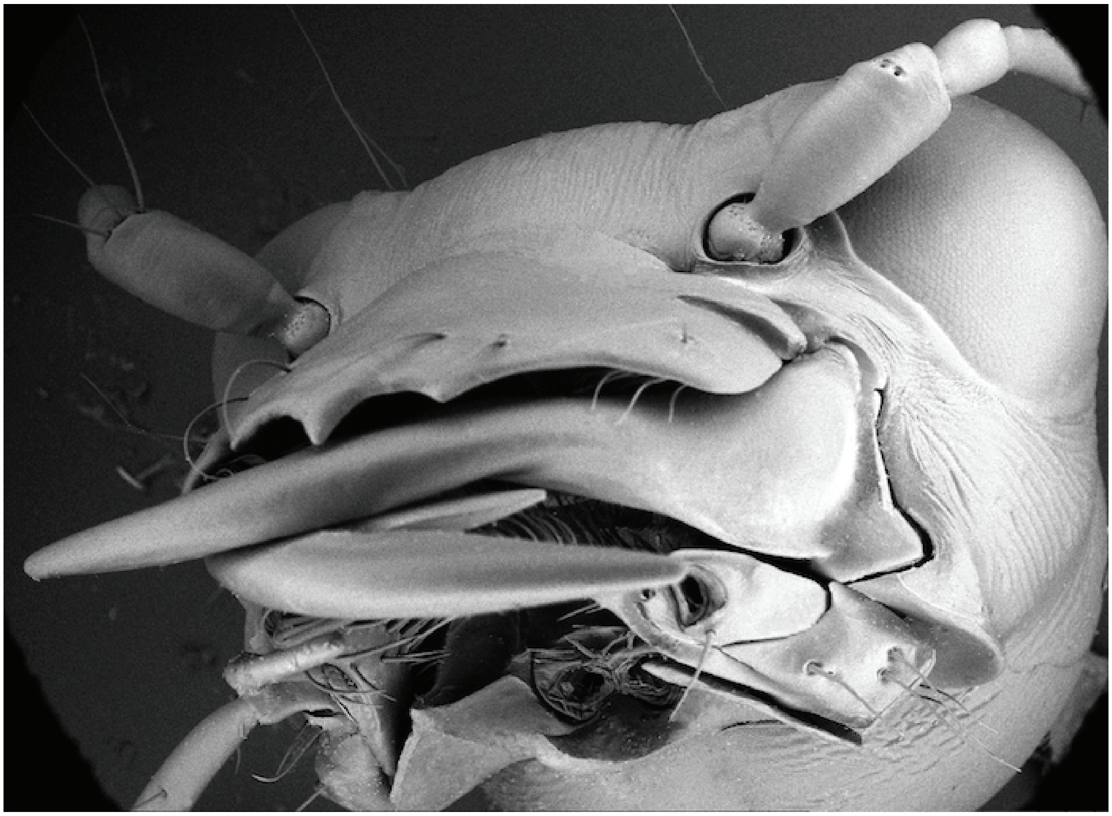


Figure 1. *Cicindela denikei*. Head-on view (x 60). The large mandibles are seen crossing each other. The base of an antenna and the eye are in the upper right quadrant.

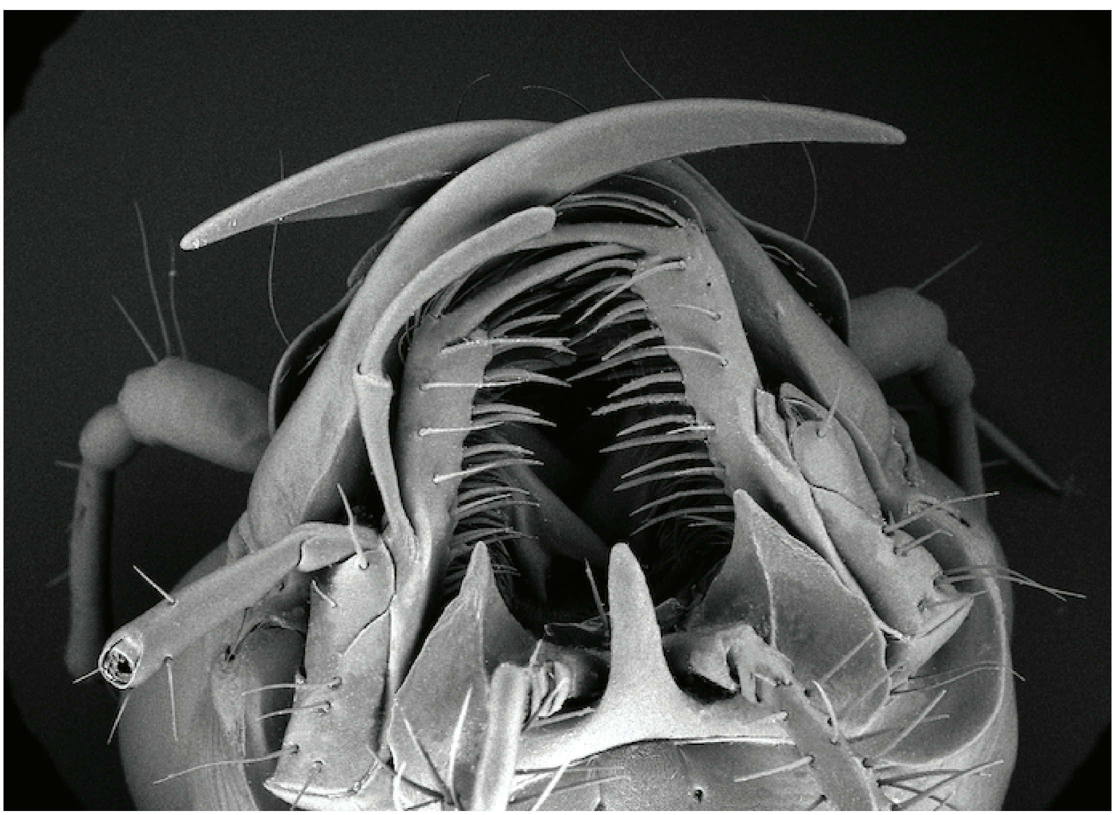


Figure 2. *Cicindela denikei*. Ventral-head view (x 60). The paired structures with bristles are the lacinia (part of the maxilla), which are employed to break down and manipulate food items.

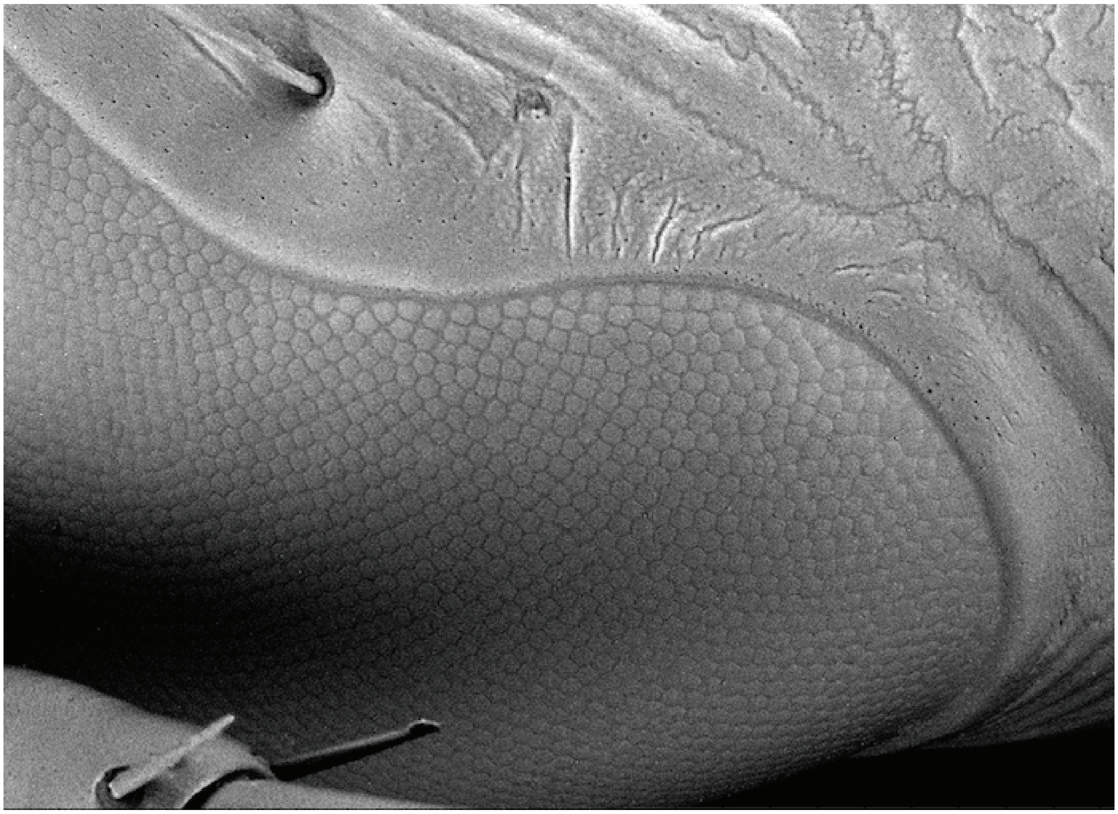


Figure 3. *Cicindela denikei*. Hexagonal facets (ommatidia) of the eye (x 200). Ommatidia photoreceptors are highly sensitive to movement and light, but resolution of the compound eye provides only mosaic images.

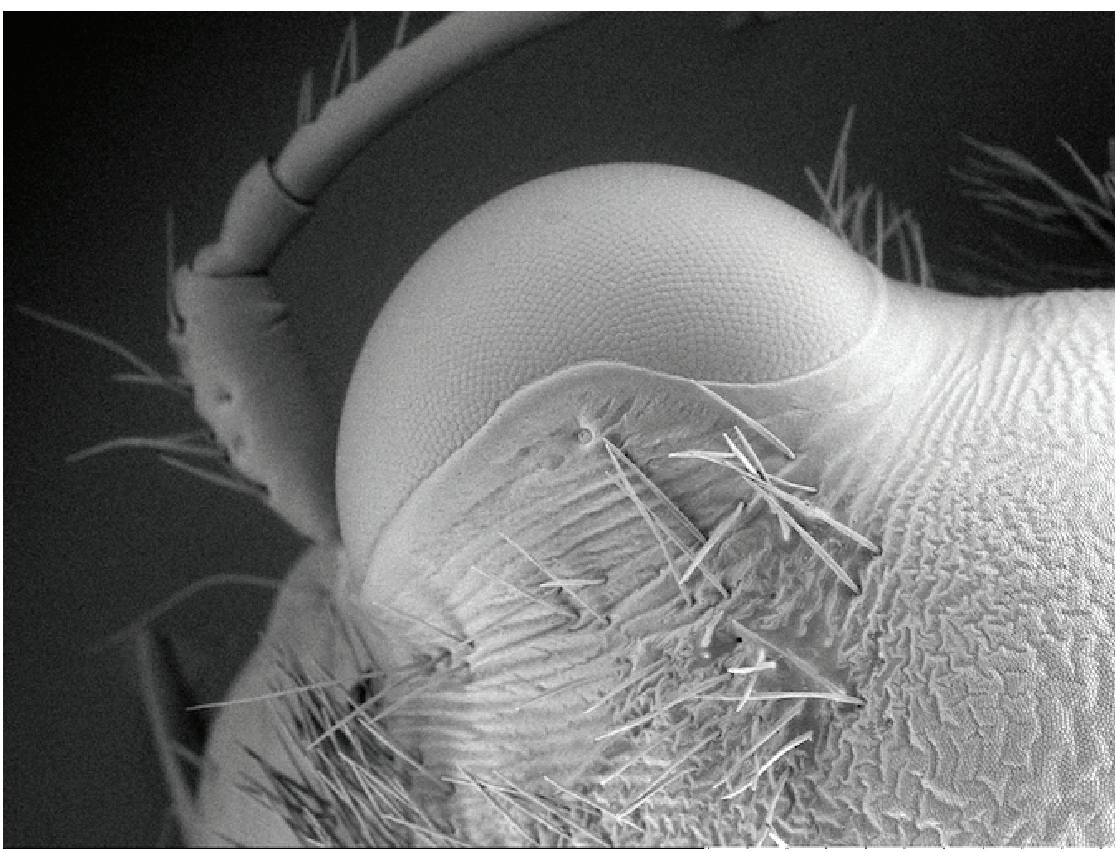


Figure 4. *Cicindela lengi*. Eye, antenna, and surrounding surface microsculpture (x 80).
Bristle-like setae provide touch sensitivity and are arranged in patterns characteristic of the species.

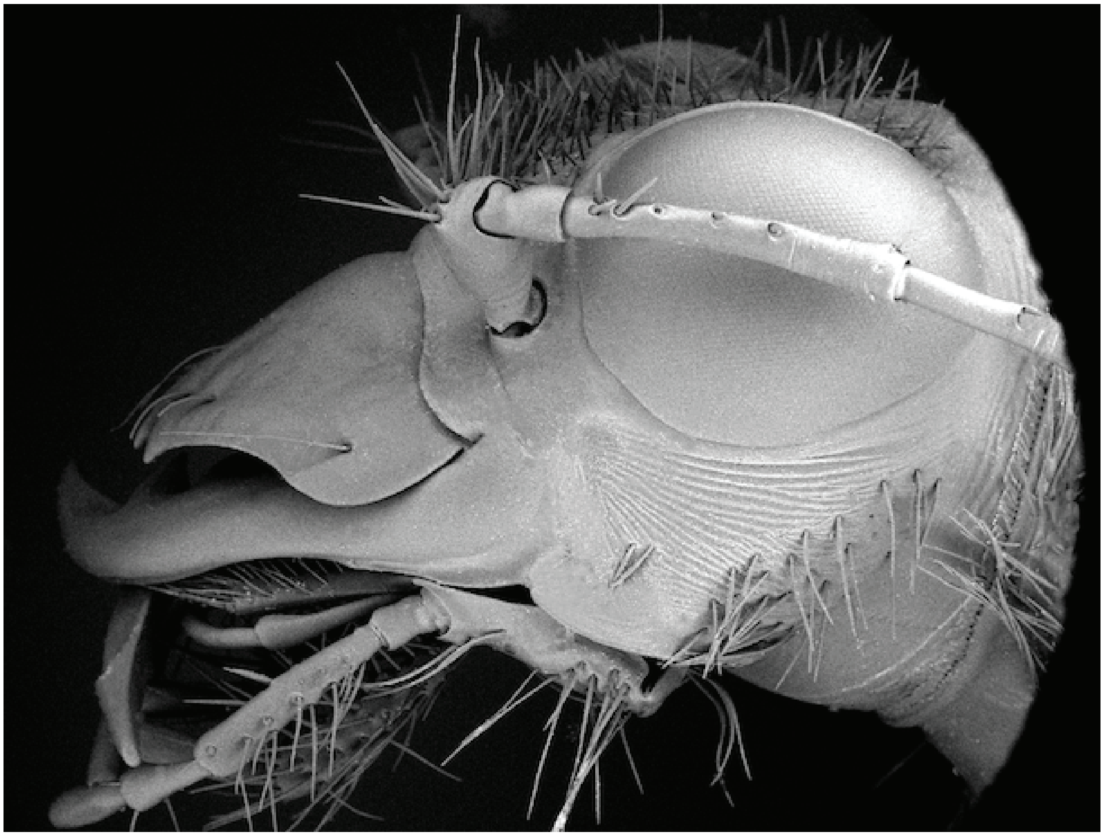


Figure 5. *Cicindela lengi*. Side view of head (x 50).

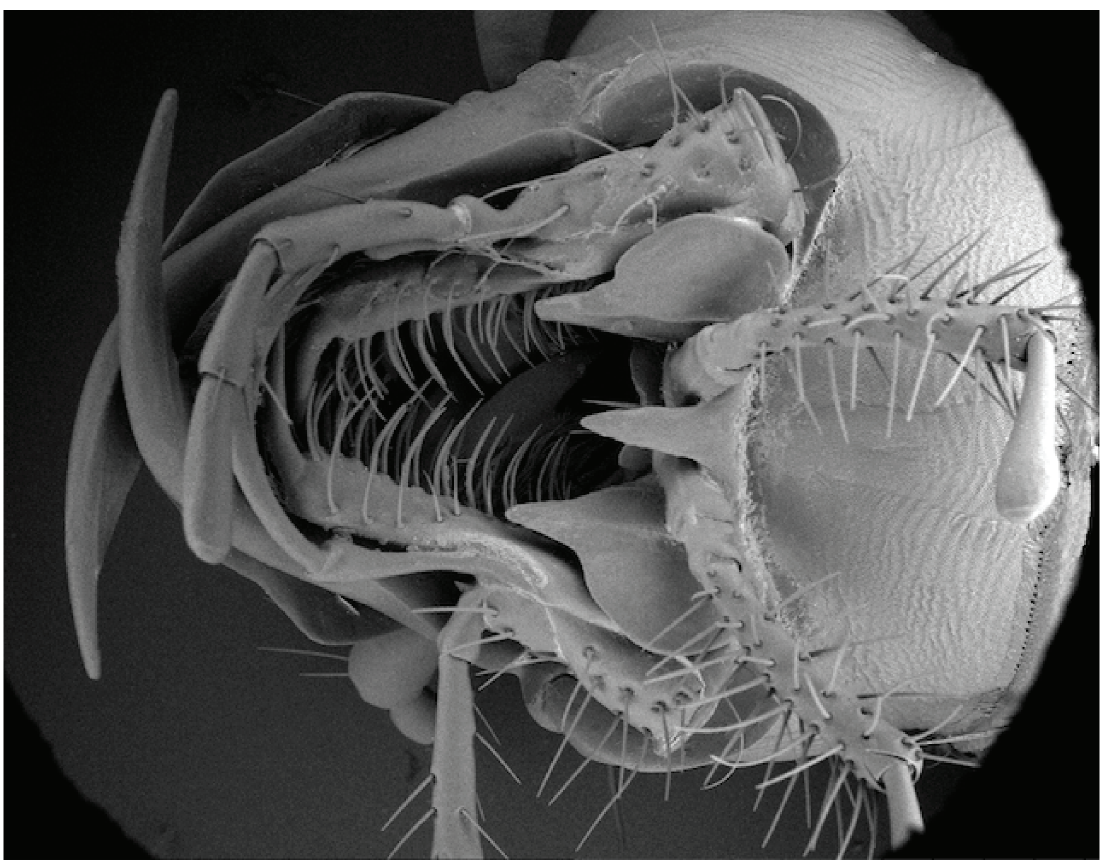


Figure 6. *Cicindela longilabris.* Ventral-head view (x 50). Three sets of palps (Maxillary, Labial and Galea) serve as touch and taste receptors, and help maneuver pieces of food and liquids toward the esophagus.

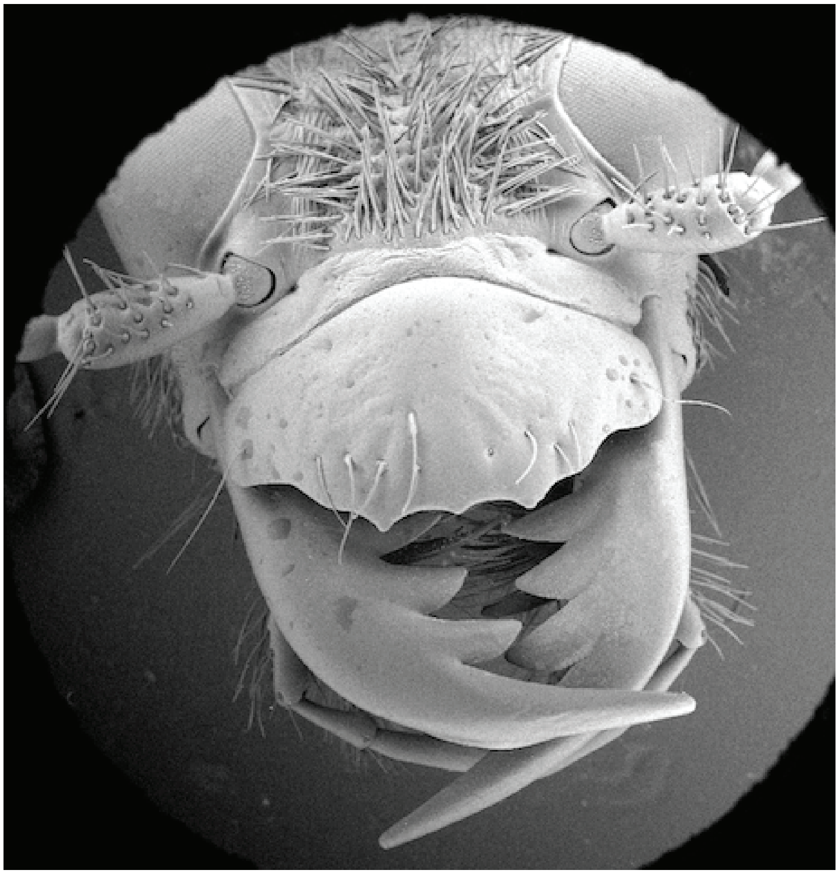


Figure 7. *Cicindela tranquebarica*. Forehead view (x 40). View reveals toothed mandibles, prominent front labrum, narrow clypeus, and frons covered in sensory setae. The ball at the base of the first antennal segment (scape) sits in a socket which permits a full-range of antennal rotation.

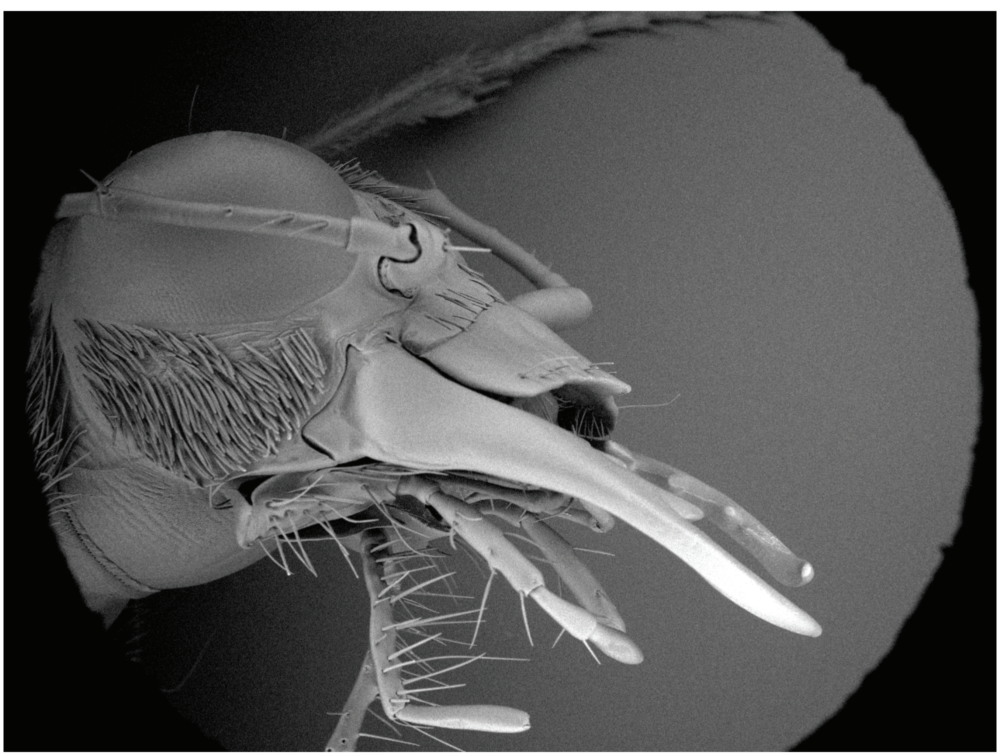


Figure 8. *Ellipsoptera lepida*. Side view of head (x 50). View shows the prominent mouthparts and eye, and the dense setae distribution typical of this species.

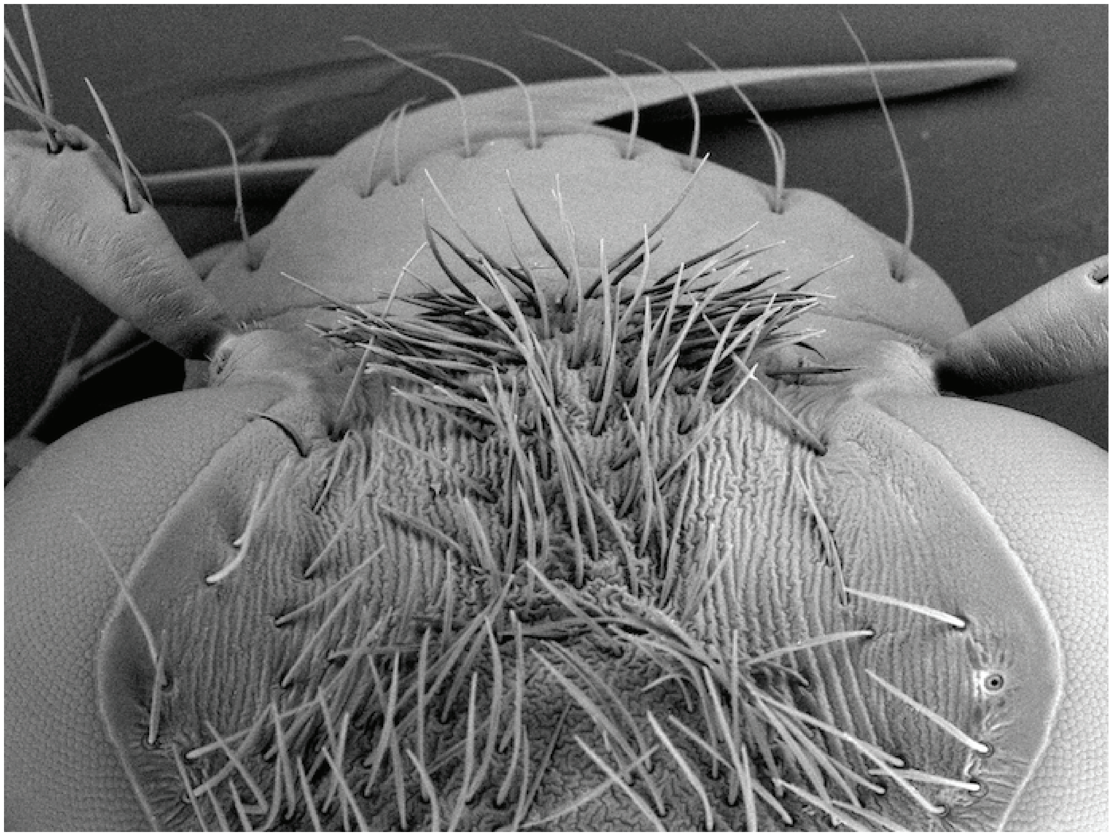


Figure 9. *Cicindela limbata*. Top view of head (x 100). The frons is densely packed with setae, each supported by a round collar. The large eyes and basal element of the antennae are present on either side of the frons.

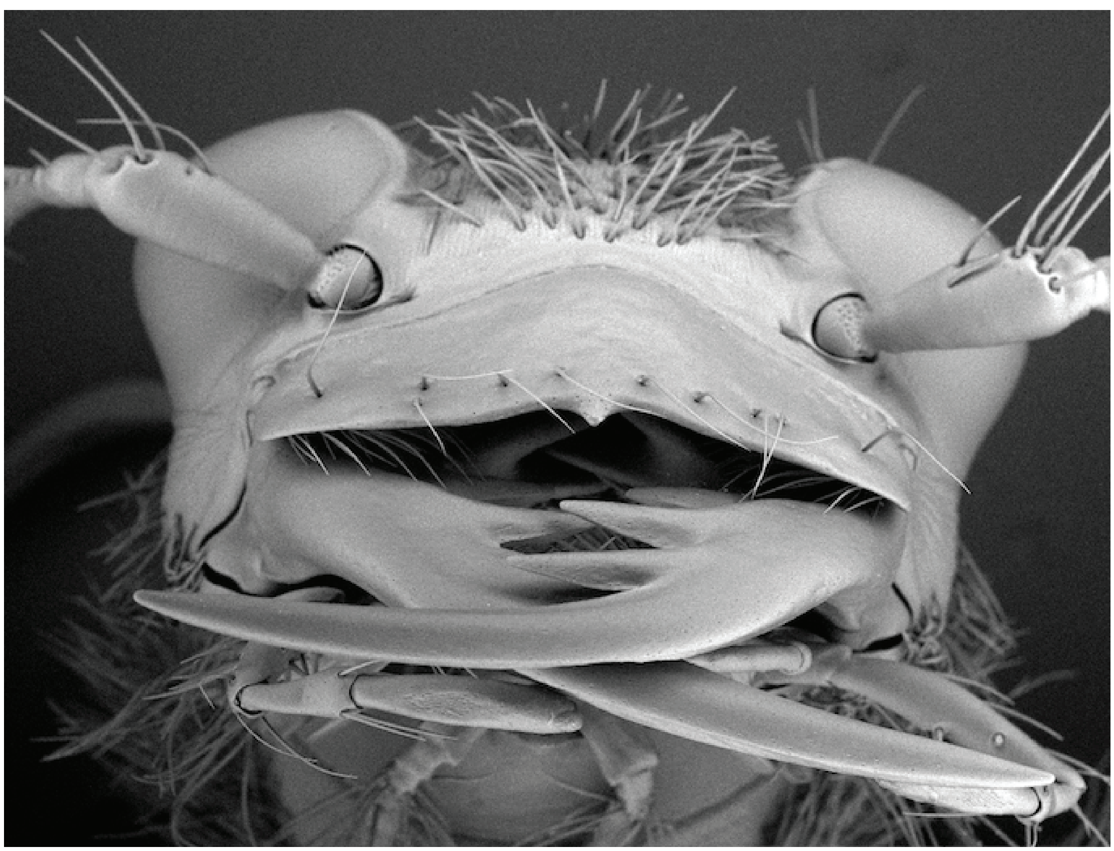


Figure 10. *Cicindela limbata*. Front view of head (x 80).

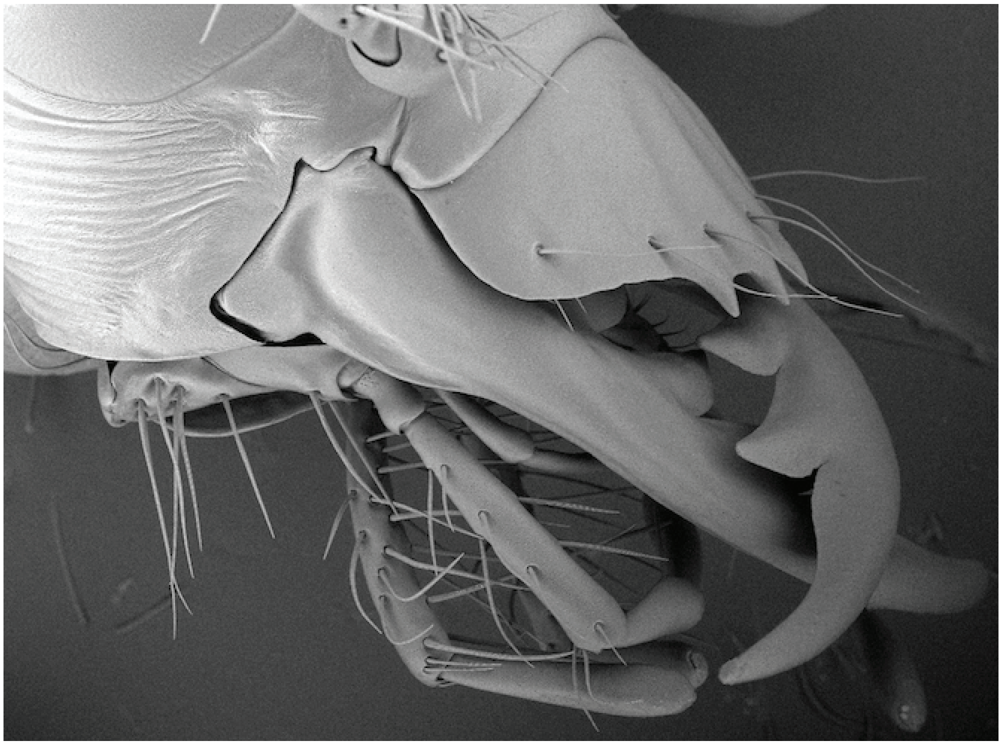


Figure 11. *Cicindela scutellaris*. Side view of head (x 80).

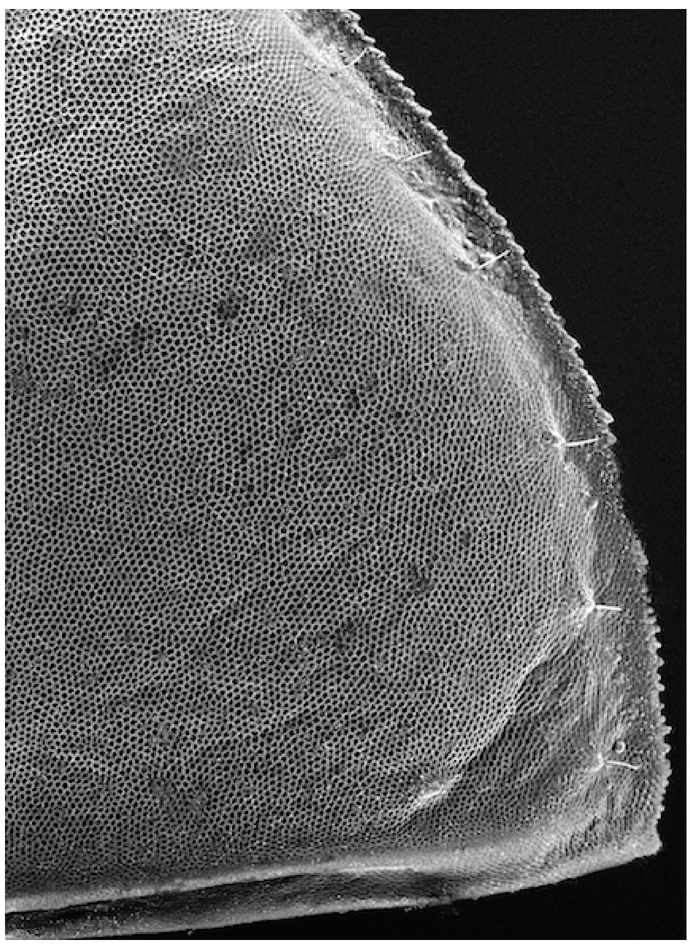


Figure 12. *Cicindela formosa*. Distal end of the right wing cover (elytron) (x 150). The microsculpture, characterized by complex latticework and multiple spaces, keeps the wing covers as light as possible.

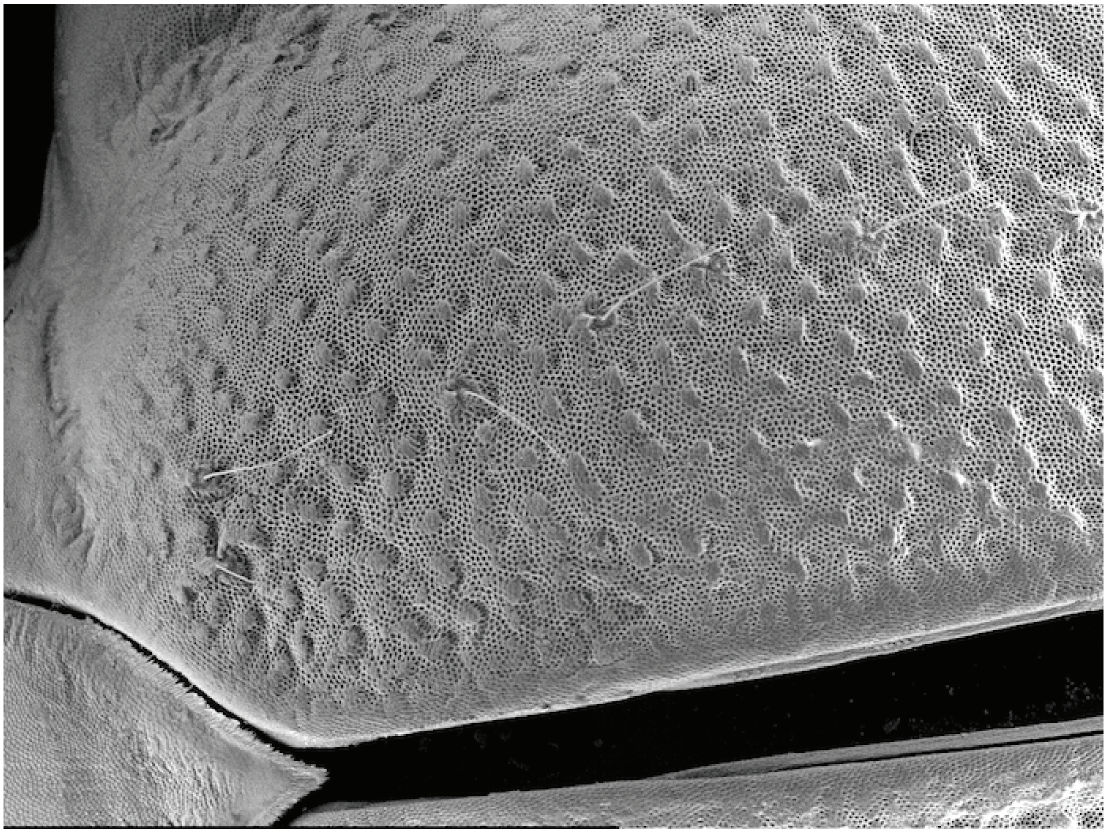


Figure 13. *Cicindela tranquebarica*. Basal end of right elytron demonstrating open latticework, knobs, and occasional setae (x 100). The triangular scutellum (the third mesothoracic tergite) is at the bottom left.

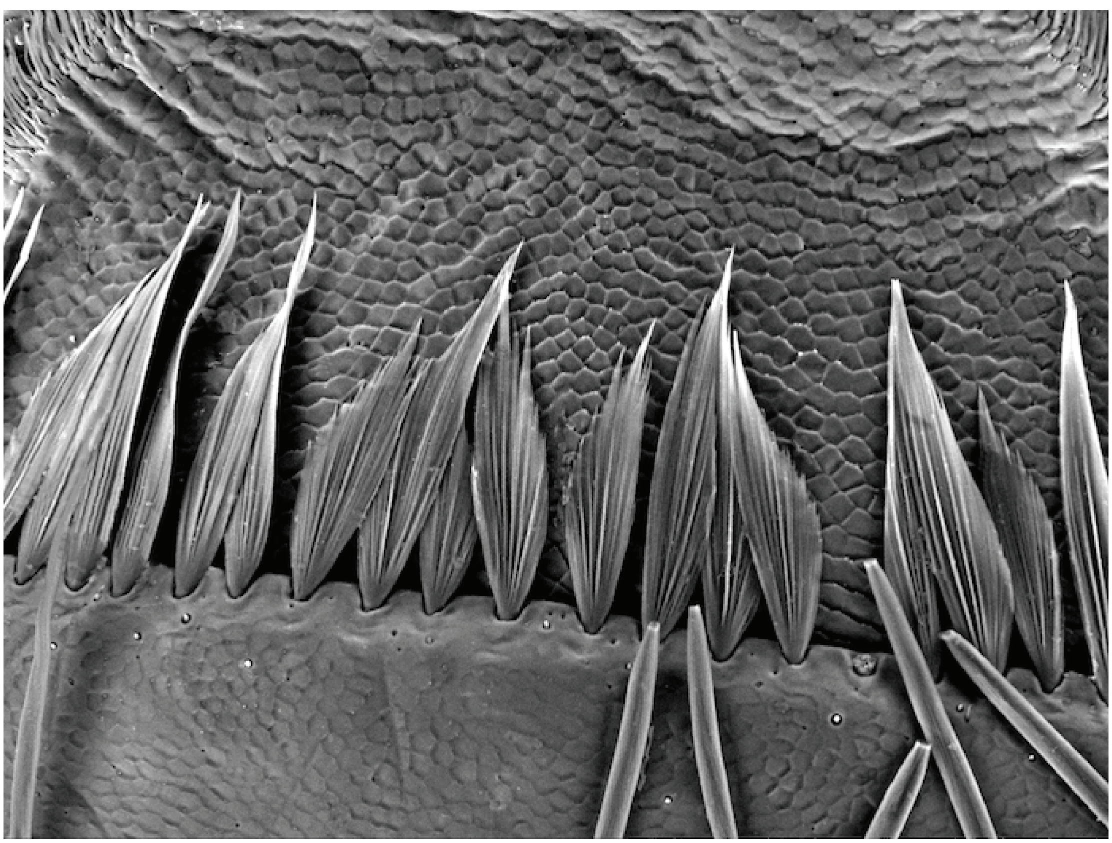


Figure 14. *Ellipsoptera lepida*. Packed setae at the back of the head extend over the scutellum (x 500).

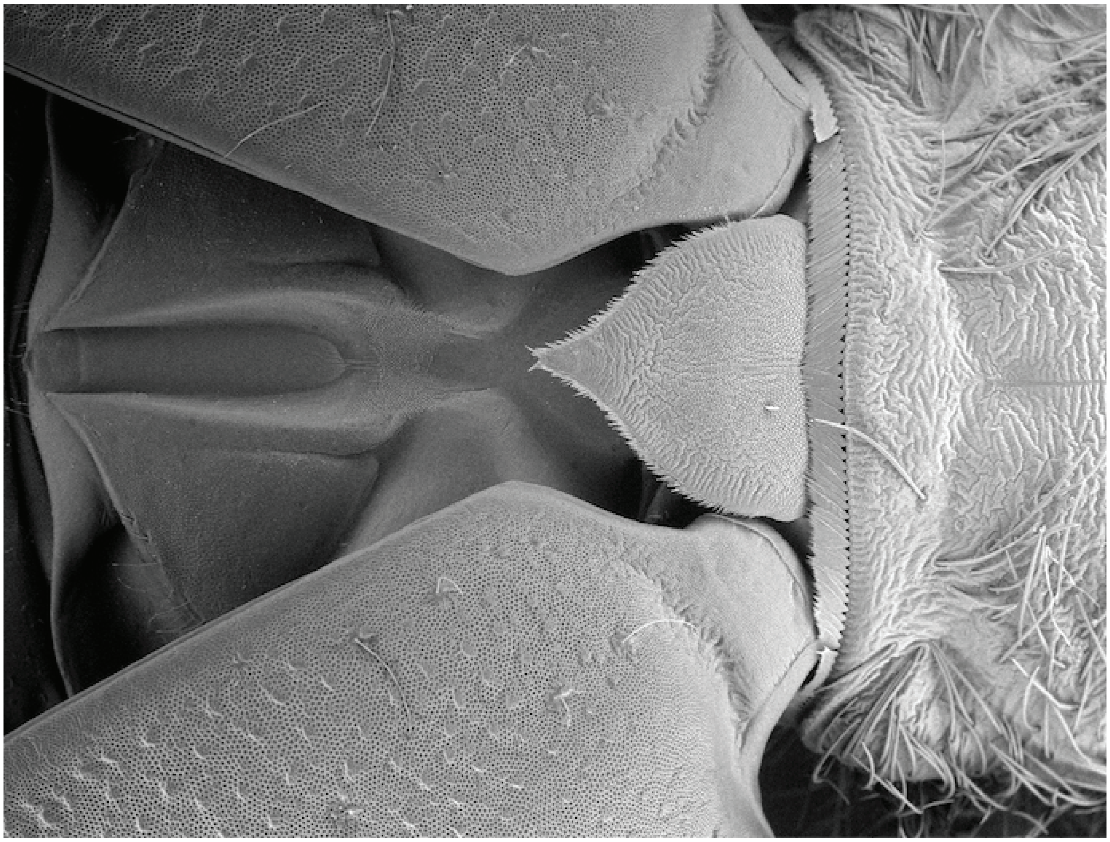


Figure 15. *Cicindela limbata*. View of the posterior of the head, the scutellum, and the open, paired elytra (x 80).

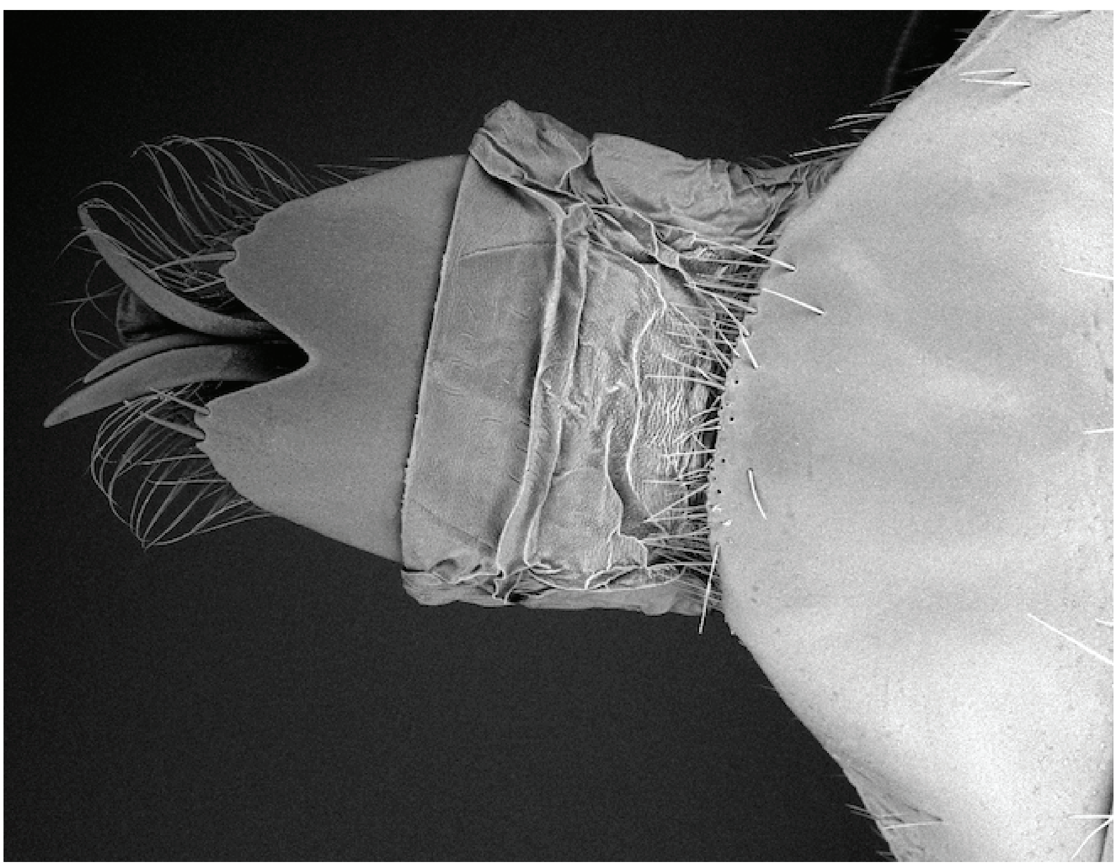


Figure 16. *Cicindela scutellaris*. External female reproductive system (composed of the eighth and ninth abdominal segments), which can be extruded as an ovipositor (x 80). The claws (styli) assist in egg deposition into the soil.

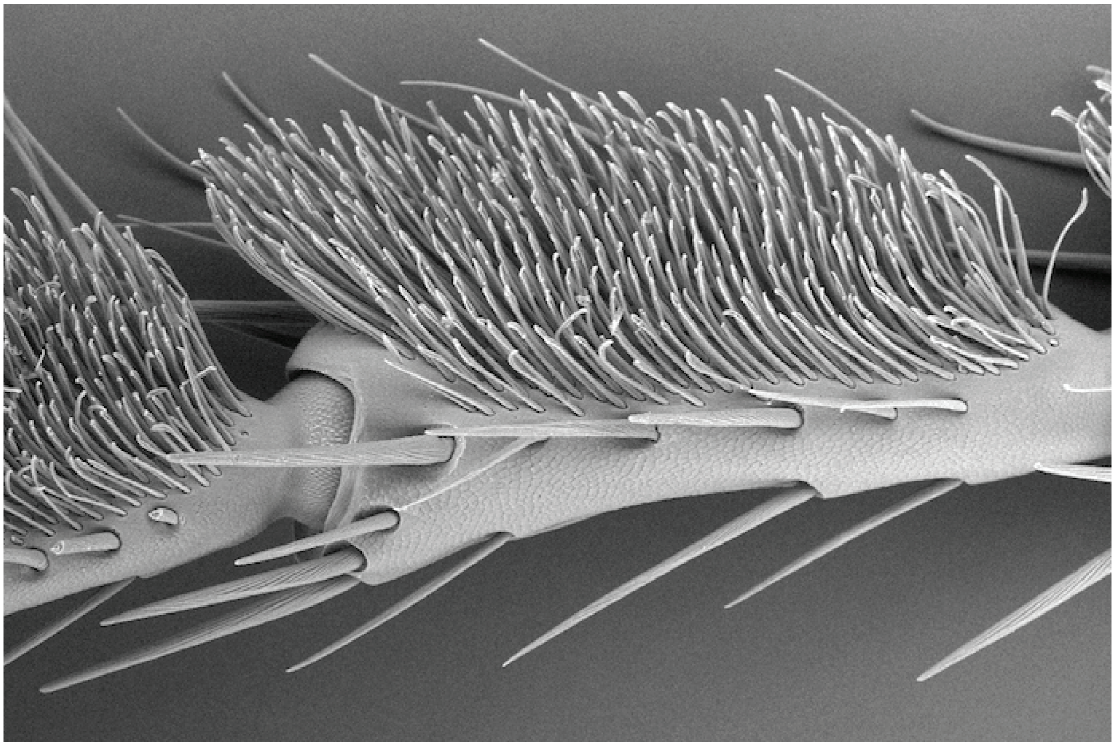


Figure 17. *Cicindela formosa*. Tarsal segment (x 500). Two types of setae are present, the long ones provide touch sensitivity, while the brush assists with traction on loose and hard surfaces. Ball-and-socket joints between the tarsal segments offer flexibility, and help absorb forces during take-off and landing.

Figure 18. *Cicindela lengi*. Components of a leg (x 50). The proximal unit is the large coxa, followed by the triangular trochanter, setiferous femur, tibia (with a prominent spur), and tarsus.

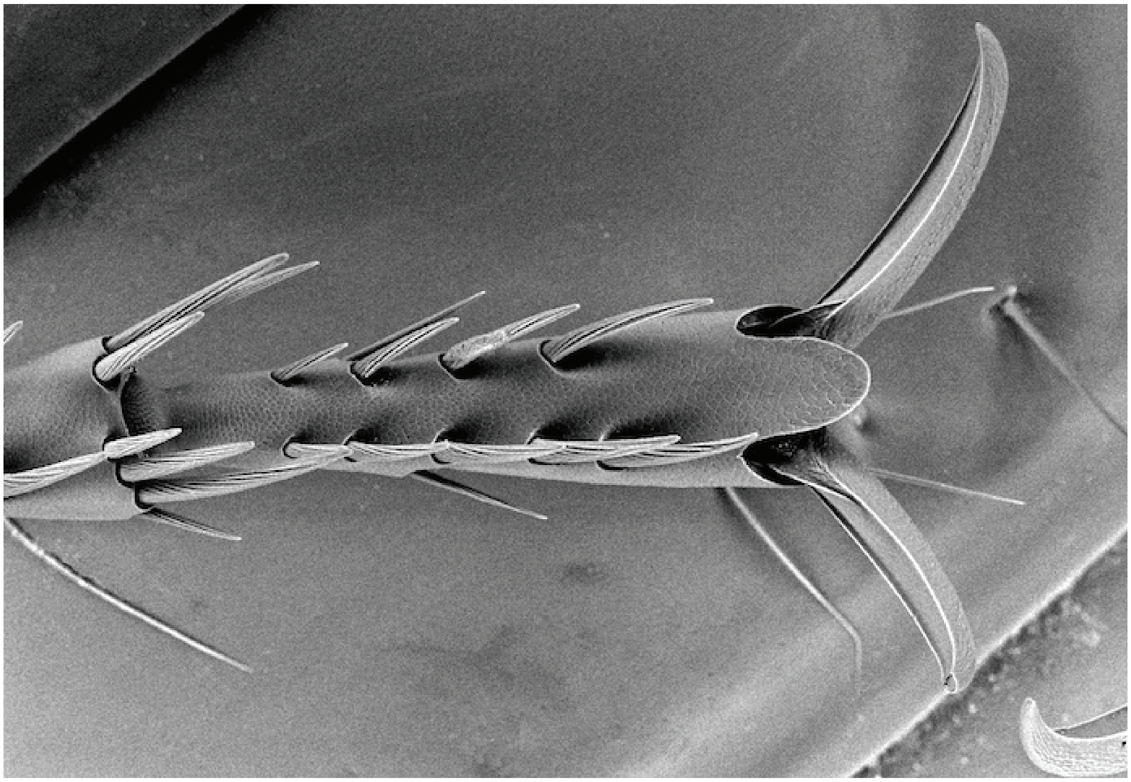


Figure 19. *Cicindela longilabris*. Fifth tarsal segment with tarsal claws (x 180). The large setae contribute to traction, while the one pair by the claws are touch sensitive.

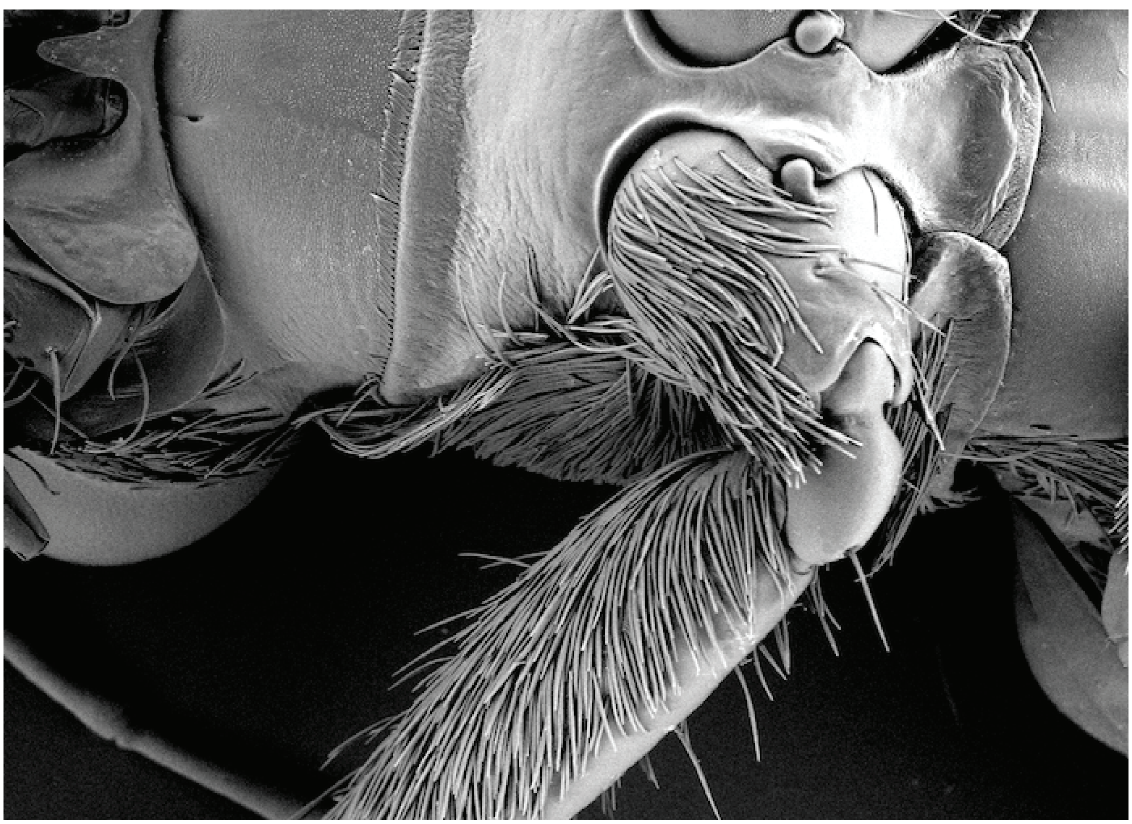


Figure 20. *Ellipsoptera lepida*. Prosternum and foreleg (x 80). Bottom of the head with an eye on the left. *E. lepida* is more-heavily covered with setae than other Manitoba species, perhaps a protective adaptation to the beetle being fully exposed for many hours of the day to the intense solar radiation in its non-vegetated habitat.

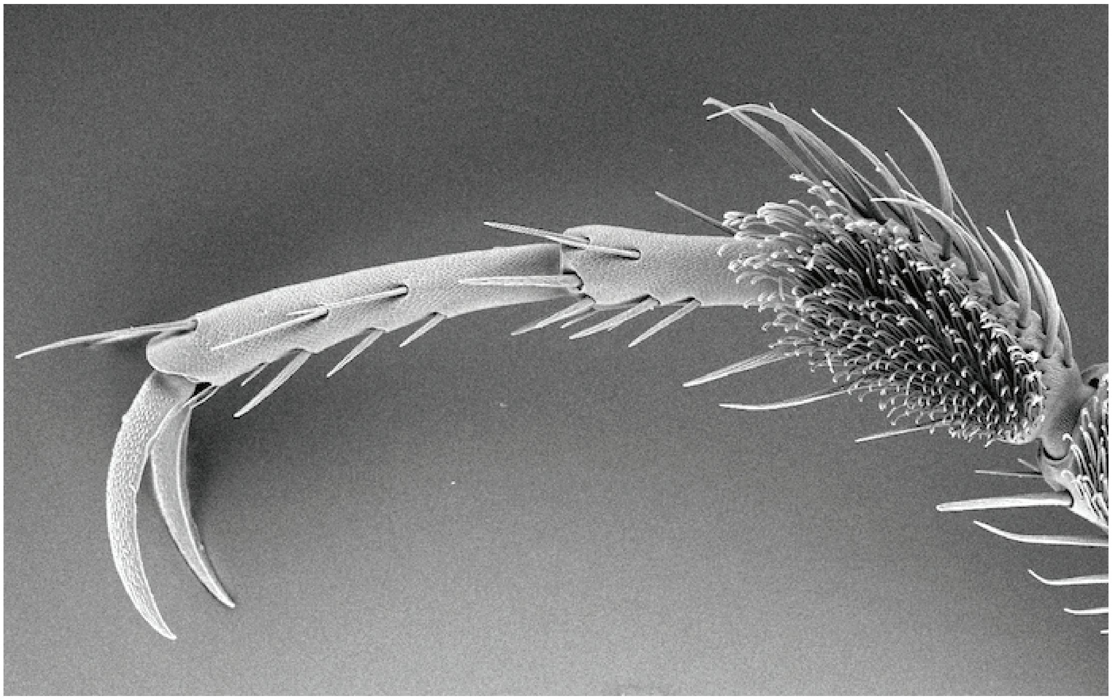


Figure 21. *Cicindela scutellaris*. Terminal three tarsal segments of a male's foreleg showing fine detail of surface structure (x 150). Note the setal pad found on the male's foreleg tarsum, which is lacking in the female. This character may be used to distinguish a male from a female tiger beetle.

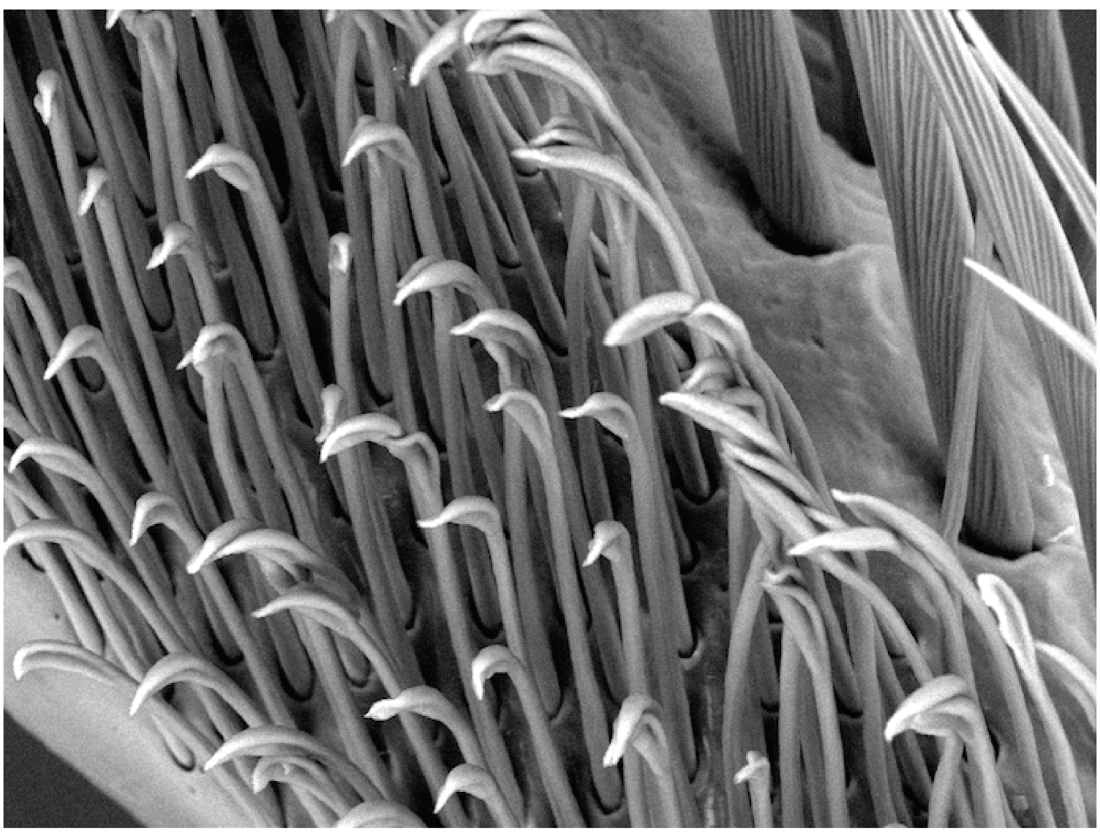


Figure 22. *Cicindela scutellaris*. Hooked setae of the tarsal pad on the male's foreleg (x 1000).

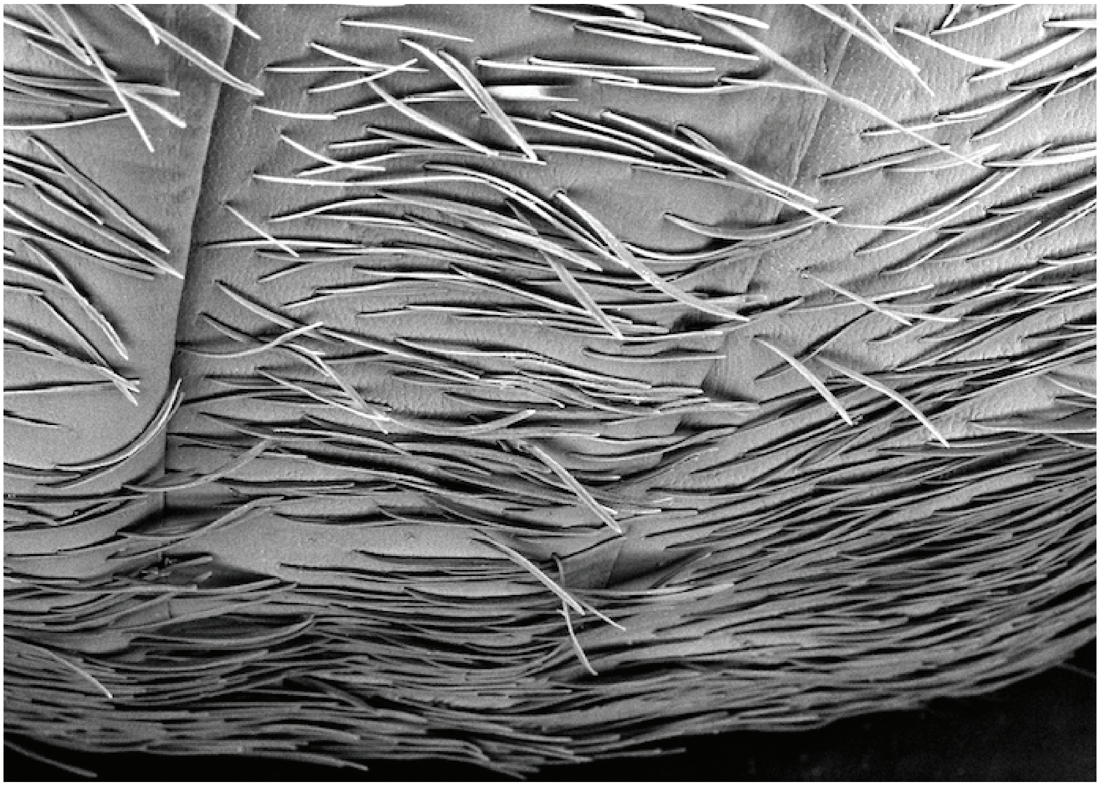


Figure 23. *Ellipsoptera lepida*. Abdominal segments generously covered with appressed setae (x 180).

Figure 24. *Cicindela limbata*. A spiracle – one of a series of respiratory openings on each side of the thoracic and abdominal segments (tergites), hidden by the elytra in repose (x 1800). The complex of finger-like projections and setae may serve in air filtration and in slowing the rate of water loss. A spiracle contains a closing apparatus, not unlike that of the stomata of plant leaves. Pumping contractions of the abdomen increase the exchange of oxygen and carbon dioxide throughout the tracheal system, into the haemolymph, and finally into cells.

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Dr. Robert E. Wrigley (© Larry de March).

Biologist Larry de March. (© Ward Christianson)

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BRONZED BEETLE ON THE BEACH

A beach -- the boundary of land, water and air.
While isolated in their states of solid, liquid and gas,
they interact in synchrony and amplify each other.
Who can resist the temptation to explore a sandy shoreline?
Certainly not a fox, minnow or tern,
as they dance in their elements and peer into each other's world.

Strolling along a beach, one becomes a child again.
Hot sand stinging the soles, cold water biting the ankles,
the wind tossing one's hair and exciting the heart.
Marvel at the sculptural mass of a gray weathered log,
the terror of a bleached pike skull picked clean, the soft curving grace of a white pelican feather.

Stark-naked tree roots, swirling stems of tall yellow grass, polished half-buried boulders,
and windrows of bright green lake weeds stranded on wet rippled sand
all reveal the awesome power of summer storms, giving way in time to restful silence.
Inhale the thick fog of an early spring morning, absorb the reddish-orange serenity of an autumn sunset,
and relish the joy of being alive and part of this Nature.

Such a sanitized and timeless place, the beach!
Repetitive tumbling and sorting of sand grains, relentlessly lapping waves and foam,
and restless winds paint awe-inspiring scenes, carried on for seconds or geological eras,
erasing each mark, burying every object, yet refreshing one's spirit.
As my steps sink into the soft sand, I glance in every direction, eagerly awaiting the next revelation.

Then along the dark damp edge of a stranded pool,
a sudden movement distracts my eye.
Was it my imagination or did something fly?
Perhaps a tiny piece of stick or reed,
under total control of a wayward breeze.

But no, there it goes again, and then again.
Capturing my curiosity by now, I approach and bend down for a closer look,
hoping to discover some new secretive delight.
A tiny cream and bronze tiger beetle, standing high on six spindly legs
stares back at me with bulging eyes, and quickly takes flight, only to vanish when it lands.

But how can it survive in such an exposed and turbulent plot?
Days spent tracking down beach flies, attempting to mate, and avoiding shore birds by hiding in the sand.
This tiger beetle's life is brief, two years at most, spent mainly in a grub-like larval stage,
hanging upright in its burrow, wide jaws spread ready, waiting for passing prey, which may or never arrive.
Just one of so many intriguing creatures pursuing its life cycle, and sharing my beach.

At the end of such a heart-warming day,
full of up-lifting thoughts, serenity and beauty,
can one walk away, back over the dunes
without regret at departing such an elysian place?

ROBERT E. WRIGLEY, Ecologist

QUOTATIONS

"Nowhere does the art of Nature manifest itself more brilliantly than in the insects...in those small, almost insignificant creatures, what functional expediency, what indescribable perfection was here provided! Where did Nature find room to lodge so many senses on the body of a gnat...But in truth, nowhere does Nature show herself so great as in the smallest of her creatures. Therefore I implore the reader, albeit he has little regard for many of the objects, nevertheless not to distain the description of them, since in observing Nature, nothing ought to be considered unimportant." (Pliny the Elder aka Gaius Plinius Secundus, CE 23-79, Naturalis Historia 77 CE)

"The sight indeed of a well-stored cabinet of insects will bring before every beholder not conversant with them, forms in endless variety, which before he would not have thought possible could exist in nature...But even this will not bring you to the end of your pleasures: you must leave the dead and visit the living; you must behold insects when full of life and activity, engaged in their several employments, practising their various arts, pursuing their armours, and preparing habitations for their progeny; you must notice the laying and kind of their eggs; their wonderful metamorphoses; their instincts, whether they be solitary or gregarious; and the other miracles of their history..."
(William Kirby and William Spence, 1815 and 1858. An Introduction to Entomology; or Elements of the Natural History of Insects.)

"Many of the Tiger beetles, although they are such conspicuous and beautiful objects in our cabinets, are well disguised when in their natural stations...I noticed generally that whatever the colour of the sand or the soil, the common Tiger beetles of the locality were of the same hue. A most remarkable instance of this was a species which I found only on the glistening, slimy mud of salt marshes, the colour and shine of which it matched so exactly that at a few yards' distance I could only detect it by the shadow it cast when the sun shone." (Alfred Russel Wallace, 1867. The Disguises of Insects; Hardwicke's Science-Gossip)

"It seems sad, that on the one hand such exquisite creatures should live out their lives and exhibit their charms only in these wild and inhospitable regions... while on the other hand, should civilized man ever each these distant lands...we may be sure that he will disturb the nicely-balance relations of organic and inorganic nature as to cause the disappearance, and finally the extinction, of these very beings whose wonderful structure and beauty he alone is fitted to appreciate and enjoy." (Alfred Russel Wallace, 1869. The Malay Archipelago)

"Many beetles are coloured so as to resemble the surfaces which they habitually frequent. Other species are ornamented with gorgeous metallic tints – for instance, many carabidae which live on the ground and have the power to defend themselves by an intensely acrid secretion...These spendid colours, which are often arranged in stripes, spots, crosses, and other elegant patterns, can hardly be beneficial, as protection...Hence the suspicion arises, that they serve as a sexual attraction; but we have no evidence on this head, for the sexes rarely differ in colour." (Charles Darwin, 1871. On the Descent of Man, and on Selection in Relation to Sex)

"It is astonishing how many different organs are worked in by nature, for the seemingly insignificant object of enabling the male to grasp the female firmly...The tarsi of the front-legs are dilated in many male beetles, or are fashioned with broad cushions of hairs...so that the male may adhere to the slippery body of the female." (Charles Darwin, 1871. On the Descent of Man, and on Selection in Relation to Sex)

"All of us are immensely indebted to those who have gone before us. The mass of knowledge about insects, great in reality but small in comparison with our ignorance, has been accumulated, bit by bit, by the laboring man in his Sunday stroll and by the highly trained investigator. I have drawn freely on books and papers, too numerous to mention, for facts which I did not previously know..."
(Frank. E. Lutz, 1918. Field Book of Insects of the United States and Canada, Aiming to Answer Common Questions)

“Young insects may be said to grow by leaps and bounds, not gradually. They are largely covered by a shell-like skin that will not stretch. All the flesh is inside of this shell, and when the quantity of this flesh gets too large the shell splits, the insect emerges, swells out, and its new skin in turn hardens. This process is repeated several times before adult life is reached.” (Frank. E. Lutz, 1918. Field Book of Insects of the United States and Canada, Aiming to Answer Common Questions)

“With increasing habitat fragmentation [of Cicindelidae], much beetle conservation is necessarily concentrated on isolated populations. Genetic appraisal to assess the distinctiveness of such populations helps to illustrate their evolutional significance and the patterns of their evolution and isolation.” (Tim R. New, 2010. Beetles in Conservation)

“I watch a tiger beetle as it runs (speediest of all insects) and takes flight without my realizing at first what a miraculous feat of synchrony I have just witnessed, involving visual perception, neural pathways, and muscle coordination – overcoming inertia, the force of gravity, air resistance, and avoidance of physical obstacles, all the while maintaining perfect balance. What exquisite mastery of both terrestrial and aerial locomotion by a tiny insect!” (Robert E. Wrigley)

Tiger beetles *(family Cicindelidae)* are highly active and elusive insects named for their voracity as predators. With keen eyesight and tracking skill, they run down moving prey and strike with lightning speed, piercing their victims repeatedly with their prominent, canine-like, multi-toothed mandibles. Another major reason for these beetles' success is their ability to exploit challenging habitats (e.g., saline mudflats and sand dunes) shunned by many other kinds of insects.

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