Rolf G. Oberprieler[1] & Erik Arndt[2]

[1]CSIRO Entomology, Canberra, Australia, [2]University of Applied Sciences, Bernburg, Germany

ON THE BIOLOGY OF *MANTICORA* FABRICIUS (COLEOPTERA: CARABIDAE: CICINDELINAE), WITH A DESCRIPTION OF THE LARVA AND TAXONOMIC NOTES

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Observations from both the field and captivity on the biology and behaviour of *Manticora* in southern Africa gathered over two decades are collated and presented under the aspects of activity patterns, locomotion, escape and defence, hunting, prey detection, prey capture and feeding, fighting, mating and mate-guarding, oviposition, sheltering and hibernation, and prey spectrum for the adult beetles, and activity patterns, tunnel construction, prey detection, prey capture and feeding, and prey spectrum for the larvae. A likely parasitoid of the larva is identified. The larvae and aspects of the hunting behaviour of adults and larvae are illustrated in colour for the first time. Contrary to earlier reports, the adults hunt their prey by smell and are opportunistic diurnal predators of phytophagous terrestrial insects, not 'snail-shell breakers' specialized to prey on strongly sclerotized beetles. The large, sexually dimorphic mandibles fulfil an additional role during mating in that they enable the male to ride on the female in a prolonged mandibular amplexus and guard her against other males. The asymmetrical development of the male mandibles appears to represent an evolutionary compromise between the selection pressures of prey capture and mate guarding. The larvae of the three common species of the genus, *M. tuberculata* de Geer, *M. mygaloides* Thomson and *M. latipennis* Waterhouse, are described in all instars. They are characterized by eight autapomorphic character states and also display some characteristics shared with the *Megacephala* group, supporting the notion of a common early split from the remaining cicindelines. It is concluded that the current classification recognizing several closely similar and largely sympatric species is untenable from a biological and evolutionary perspective and that, in addition to the above-mentioned species, only *M. congoensis* Péringuey and *M. gruti* Boucard appear to represent natural but allopatric species. A thorough and comprehensive systematic revision of the genus is required to fully clarify its taxonomy.
Correspondence: R. Oberprieler, Division of Entomology, CSIRO, G.P.O. Box 1700, Canberra, ACT 2601, Australia. E-mail: rolf.oberprieler@ento.csiro.au
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Despite the interest that the large southern African tiger beetles of the genus *Manticora* have generated for more than a century among students and collectors of tiger beetles, little is known about their biology and ecology. Yet, in view of the basal phylogenetic position of the genus (Arndt & Putchkov 1997), knowledge of its larva and larval habits is crucial to understanding its relationships to other cicindeline genera. Unfortunately also, much of the scanty biological information that has been published on these beetles is unsubstantiated or incorrect, as shown by the senior author's observations in the field and laboratory in southern Africa over a period of twenty years. This paper collates all the behavioural observations of *Manticora* obtained from mainly three populations representing (according to the current state of taxonomy of the genus) two species. Descriptions of all three larval instars of the genus are provided, based on specimens from these and some other recently sampled populations. Finally, the function of the enlarged mandibles in the males and the bearing of differences in characters of the larvae and of behavioural traits on the taxonomy and species boundaries in the genus are discussed.

Sketchy early biological notes on *Manticora* were published by Castelnau (1863), Lucas (1883) and Simon (1894). Péringuey (1893) provided a more detailed account of the habits of adult *Manticora*, his observations and interpretations being, in comparison with those of later authors, remarkably acute and accurate, if somewhat anthropomorphic (' … perched high on their legs [they] move about in the dry barren plains of the Karoo, in a jerky impetuous manner, which implies a bold, fearless temper, evidently aware of its physical power.', p. 3). Although Péringuey could not ascertain the precise identity of the natural prey species of these beetles, he judiciously suspected that a common grasshopper and termites served as the principal food of the adults and larvae, respectively. He also noticed the sexual dimorphism of the mandibles and recognized that their greater development in the male 'has probably been acquired for the purpose of seizing hold, as they do, of the broad neck of the female for mating'. Perhaps most significantly, he realized that the great variability in size and development of characters in these wingless beetles is largely due to their limited vagility and consequent isolation of populations, as well as to greatly varying climatic conditions and availability of food in their generally drought-prone habitats.

Later authors were less astute and careful in their observations and interpretations of the habits of *Manticora*. Poulton & Marshall (1902) compared it with the similar-sized and -coloured genus *Anthia* (Carabidae) and argued that it has 'a similar warning attitude … but it cannot project its protective secretion, which merely exudes when it is handled; the liquid also is not acid as in *Anthia*, but possesses a strong smell.' – a complete fabrication since *Manticora* does not exude any noticeable defensive secretion. Thiele (1977) portrayed *Manticora* as representing an extreme case of 'procerization', as typical in snail-shell breaking carabids, and suggested the large development of its mandibles to be an adaptation to particularly large and resistant prey such as scorpions – in total ignorance of the evident sexual dimorphism of these structures. Roer (1984), who published the most comprehensive study of *Manticora* behaviour to date, refuted Thiele's hypothesis that these beetles are specialized scorpion predators in a laboratory experiment. However, he espoused the 'snail-shell breaker concept', applying it instead to strongly sclerotized prey such as apterous, terrestrial tenebrionid beetles (even though his own experiments demonstrated that *Manticora* cannot crush sclerotized *Onymacris* species). Further, he alleged that *Manticora* is essentially a nocturnal hunter that tracks its prey visually – apart from being almost contradictory, both these statements are incorrect. Pearson (1988), in his general review of tiger beetle biology, treated *Manticora* only in passing

as one of the few totally nocturnal cicindeline genera, but at least did not perpetuate the 'snail-shell breaker' myth. Rather, his summary of the mandibular amplexus and contact-guarding of females by male tiger beetles implicitly applies to *Manticora* as well and is in agreement with both Péringuey's (1893) early observations and with our own conclusions regarding the function of the apparently allometrically developed mandibles of the males (see below).

Oberprieler & Grobbelaar (1991) published a preliminary, popular version of the observations on *M. latipennis* Waterhouse, detailed below, sketching the general life history and behaviour of the genus. Werner & Wiesner (1995) added a (correct) observation on the daily activity period of *M. mygaloides* ('*damarensis*') and a vague one as 'hunting for myrmopods and [the tenebrionid] *Psammodes vialis*'.

The first (but superficial) description of a larva of *Manticora* was given by Kolbe (1885), based on a specimen from the 'Mission Barmen in Afr. merid. occid.' (evidently the present Gross-Barmen near Okahandja in Namibia, 22.05S 16.44E) assignable to *M. mygaloides* Thomson (see taxonomic notes below). Shortly afterwards, Péringuey (1893) described the larva of *M. tuberculata* de Geer from Vanwyksvlei in the Cape Province of South Africa (30.21S 21.49E). Horn (1915) illustrated a larva of *M. tuberculata tibialis* Boheman but gave no proper description nor details of its origin (but see Material examined). Much later, Leffler (1980) described a defective larva of *M. latipennis* from Beira in Mozambique (19.50S 34.55E), but some of the characters he described are evidently incorrect (see below). Putchkov & Arndt (1994) included *Manticora* in their key to all known tiger beetle larvae and illustrated several important characters.

MATERIAL AND METHODS

Populations studied

The observations reported here were undertaken over a period of twenty years both in the field in the natural habitats of these beetles as well as in captivity in Pretoria, South Africa. Adult beetles and larvae from several populations were kept in captivity almost continuously from 1984 to 1996. Detailed observations and experiments were carried out from one population in the Northern Cape Province and two in the former Transvaal Province (currently Northern Province and Gauteng) of South Africa, with additional observations from populations in northern and central Namibia and the Northern Cape Province and the Northern Province of South Africa.

Our first observations were by the senior author on a population of *M. mygaloides* (form *livingstoni* Castelnau, see below) near Namutoni, Etosha Game Reserve, Namibia, in January 1976 and February 1977

(the latter recorded by Werner & Wiesner [1994] under *M. damarensis*). These observations were limited to the running, escape and feeding behaviour of adult beetles and include one of only three records of natural prey items for *Manticora.*

In December 1984, field observations were carried out by the senior author on a population of *M. mygaloides* occurring in a strip of red Kalahari soil at Pniel near Barkly West, Northern Cape Province. These observations occurred in the morning after a rainy night and covered hunting, escape, sheltering, mating and oviposition behaviour of the adults. No larvae were found, and no adults were encountered during collecting activities in the area the following night. A pair of beetles from this population was subsequently kept in a terrarium in Pretoria for nearly three years, and in April 1986 two larvae emerged from eggs laid by the female. These larvae survived to the second and early third instars, respectively.

A dense population of *M. latipennis* was found by the senior author in January 1987 in the Waterberge between Melkrivier and Lapalala Nature Reserve, Northern Province, located in a large valley of sandy *Terminalia* veld between sandstone and granite hills. Superficial observations on the behaviour of the adult beetles were made. The same population was studied in more detail in the field for two days during January 1991, covering observations of adult beetles running, escaping, digging shelters, fighting and mating. Larvae of all three instars and their tunnels were excavated from the shoulders of a gravel road, where they were particularly numerous, and some observations were made on their behaviour. Five males, three females and a number of larvae were taken to Pretoria and kept in captivity for several years, although the larvae did not survive long and none pupated. Further visits to the same locality at the same season in later years to complete and extend these observations were unsuccessful, as no beetles or larvae were found. However, adults from this population were obtained for observation in captivity during other months of later years, i.e. November, December and March, generally following extensive rains in the area.

An expedition to the Richtersveld in the Northern Cape Province in October 1991 allowed the senior author to make limited observations on the behaviour of adult *M. tuberculata* at the Ploegberg (28.38S 17.01E). In December of the same year, a very small population of *M. mygaloides* was located on the eastern outskirts of Pretoria (Elliot Ridge, Bronberge) restricted to some grazing paddocks and roadsides in the narrow strip of sandy *Burkea* veld along the foot of the northern slopes of the ridge. This population was regularly monitored during the summers of the following years until 1995, when alterations to the road and then housing development on the main paddock apparently exterminated it. However, even before these events no adults were to be found in some years, perhaps partly due to ill-timed visits but possibly as a result of poorer rainy seasons. Larvae were found only in December 1992 and 1994, again occurring together in all three instars. Both adults and larvae from this population were kept in captivity for varying lengths of time.

The junior author excavated and measured a number of larval tunnels of *M. latipennis* near Tshipise, Northern Province, in December 1996 and of *M. mygaloides (livingstoni)* in the Waterberg National Park, Namibia, in March 1998.

Conditions for observations and rearing in captivity

In Pretoria the beetles were kept in large (1200 x400 mm, 400 mm deep) glass tanks filled with sandy soil taken mostly from the habitat of *M. mygaloides* at Bronberge described above. The containers were placed outdoors to expose the beetles to natural climatic conditions and enable them to maintain their circadian and seasonal activity patterns. However, these terraria were only poor simulations of the natural environment of the beetles, since they were not nearly large and deep enough to provide the correct temperature and humidity both above and inside the soil. They were placed so as to provide sun in the morning and afternoon but shade at noon and were protected from excessive rain. Stones, dead wood and grass tufts were added as shelter for the beetles. Water was provided during prolonged dry periods but not on a permanent basis.

The beetles were mostly kept in single pairs per container, but also in combinations of two males and one female or 2-4 specimens of the same sex, so as to study particularly the interactions between the males in the presence or absence of a female. Gravid females seen attempting to oviposit were kept isolated from both males and other females. In one experiment, males from the Lapalala (*M. latipennis*) and Pretoria (*M. mygaloides*) populations were kept together to study interactions between these two taxa.

Captive larvae were reared singly, initially in soil-filled, plastic 2l drink bottles with the neck cut off and drainage holes provided in the bottom. On reaching the third instar, they were transferred to larger metal tins 500 mm deep. The limited success achieved with this larval breeding programme (i.e. the failure of the larvae to pupate) indicates that the larvae are much more sensitive to artificial conditions than the adults. However, it takes an ambitious experimental design to emulate in captivity the precise conditions, which the mature larvae experience at a depth of up to 1 m at the bottom of their widely spiralling tunnels.

Material examined for description of larvae

L_1, L_2 and L_3 refer to the larval instars I, II and III. *Manticora tuberculata (tibialis)*: $1L_1$ $3L_2$ $3L_3$, South Africa, Kimberley, 1911, J.H. Power (DEI); *Manticora mygaloides* Thomson: $1L_3$ South Africa, Pniel, 5km S Barkly West, 28.35S.24.32E, xi.1986, R.G. Oberprieler (SANC); $1L_3$ South Africa, Pretoria, Bronberge, Elliot Ridge, 25.47S 28.21E, 1400m, 28.xii.1992, R.G. Oberprieler (SANC); *Manticora mygaloides* (*livingstoni*): $5L_1$ $2L_2$ $2L_3$ Namibia, Waterberg National Park, 20.30S 17.14E, 11./12.iii.1998, E. Arndt (CEA); *Manticora latipennis:* $1L_3$ South Africa, Waterberge, Lapalala Nature Reserve, 23.51S 28.17E, 11.i.1991, R.G. Oberprieler (SANC); $4L_1$ $4L_2$ $2L_3$ South Africa, Tshipise, 22.37S 30.10E, 24./25.xi.1996, E. Arndt (CEA).

All specimens are preserved in 70% ethanol and deposited in the National Collection of Insects, Plant Protection Research Institute, Pretoria (SANC), the German Entomological Institute, Eberswalde (DEI) and the collection of the junior author (CEA). Voucher specimens of corresponding adults and also adult beetles from other populations studied are deposited in the same collections, and a few representatives also in the Australian National Insect Collection, Canberra (ANIC). The specimens of *M. tuberculata* (*tibialis*) examined are evidently those from which Horn (1915) prepared his illustrations, although he did not indicate their origin. The larvae on which Kolbe (1885) and Péringuey (1893) based their respective descriptions could not be obtained for comparative purposes and are apparently lost, as neither the Museum für Naturkunde of the Humboldt University in Berlin (Kolbe) nor the South African Museum in Cape Town (Péringuey) houses any such specimens (for the latter, H. Robertson, pers. com.). Larvae of 29 other cicindeline genera (representing all tribes) were available for comparison.

Terminology

Morphological terminology follows Putchkov & Arndt (1994) except that, in the posterior part of the parietale, 'sclerotized keel' is used instead of 'caudal ridge'. Chaetotaxy follows Bousquet & Goulet (1984). The frequently mentioned setal group gMX is located dorsally on the stipes. Measurements are given in Table 1.

RESULTS

Behaviour of the adult beetle

Activity pattern

The adult beetles generally have a bimodal activity pattern, becoming active in the early morning shortly after sunrise until about 10h00 and again in the late afternoon from about 17h00 until shortly after sun-set, before the onset of total darkness. However, this pattern varies greatly according to prevailing weather conditions. During very hot and dry days, the beetles may not become active in the morning and only emerge for a short period around dusk, or not at all for several days if the dry weather persists. During cooler, overcast days (e.g. after heavy rains) they may extend their morning activity until nearly noon and also emerge earlier in the afternoon.

Contrary to Roer's (1984) and Pearson's (1988) assertions, *Manticora* is not nocturnal. In twelve years of keeping these beetles in captivity, they almost always retreated to their shelters before it became completely dark. Exceptions were nights when termites or other mass-emerging prey insect species swarmed at dusk and continued to do so into the dark; *Manticora* would then continue preying on these until it could feed no more, before retreating to a shelter for the night. Also, on numerous nights of collecting insects in *Manticora* habitats in southern Africa, including the localities of all the populations here studied, no adults were ever seen hunting at night. Similarly, they were never encountered visiting light-traps, as *Megacephala* often does. It is possible that some nocturnal hunting may take place occasionally, as implied by Roer (1984) and Werner & Wiesner (1995), such as during full moon or following evening rain after a long period of drought, but in general *Manticora* is active in the early morning and late afternoon and not nocturnal, nor even crepuscular. The reason for this activity pattern is unclear; it may be linked to that of the predominant prey species, to competition from large nocturnal carabids such as *Anthia*, or possibly to predation pressure by owls (which regularly prey on nocturnal arthropods such as scorpions, solifuges, crickets and large beetles, and which *Manticora* would not be able to detect and escape, see below).

Locomotion, escape/defence and hunting

Manticora is a fast and agile runner. The long legs lift the short body high off the ground so that the beetle can easily negotiate small obstacles without losing momentum or direction. Its movement is not as fast-spurting as that of smaller cicindelines such as *Dromica* or the winged *Lophyra* and relatives, but it can maintain its speed for a longer period, especially when trying to escape from a potential predator. This, together with its ability to stop or change direction rapidly, makes it difficult to catch once alarmed, both for humans and for larger insectivorous birds.

It seems that such birds (predominantly rollers, hornbills, shrikes and kites) constitute the main predators of these beetles, since the latter are alert to movements of large objects and shadows falling over them. Such enemies are evidently detected visually, and the beetle then tries to escape by running rapidly

for shelter among vegetation, its movement jerky with frequent brief stops and changes of directions. When cornered, it raises its forequarters and opens its mandibles in a threatening gesture, biting-releasing whenever it is touched. Its eyesight is evidently too poor to detect and counter a directed attack; instead it only reacts to general movements of the attacker. No direct observations of *Manticora* being preyed upon are available, however.

When searching for prey, the beetle runs relatively slowly though erratically, moving about in a more or less zigzag fashion with the head held low. The ground and objects on it, such as grass tufts and stones, are probed with the antennae, which are held out at about 45º from the body axis (figs 1, 2). It periodically pauses with a peculiar, fast, sideways-quivering motion of the body, remaining perched high on its legs and motionless for a brief period (fig. 2). Before moving on again, it usually cleans its antennae by pulling them through the cleaning organs on the front tibiae.

Prey detection, prey capture and feeding

Contrary to Roer's (1984) assertion, *Manticora* does not detect its prey visually. Its eyes, although rather prominent, are comparatively much smaller than those of smaller cicindelines which hunt visually, and it has become evident both from observations in the field and trials in captivity that their sight is too poor to identify even large and moving prey. Instead, *Manticora* evidently detects its prey by means of a keen sense of smell located on the antennae. These constantly probe the ground in front of the beetle for the scent of prey, and the beetles are even able to follow a scent trail. When a *Manticora* detects the odour of a prey, it becomes highly agitated and runs about with sideways-sweeping motions of its forequarters so as to locate the strongest scent concentration, antennae trembling and mandibles agape. In this direction it charges forward, constantly adjusting its way as it follows the trail. As the scent grows stronger, the beetle becomes ever more frantic, scrambling over the ground in a rather uncoordinated fashion.

When it reaches the prey, it pounces on it with its front and middle legs and delivers a crushing, downward bite with its strong mandibles (fig. 3). If this bite is not effective, such as when delivered to the posterior of the prey, *Manticora* will release its grip and quickly seize the prey again, aiming for the neck and then holding and squeezing it for a while. If the prey is large and continues to struggle, the beetle will slightly release its grip, allowing the prey to move out of the grasp for a short distance before the beetle bites down hard again. In this way the prey is gradually crushed.

When the prey becomes motionless, *Manticora* carefully releases its grip and rotates the victim with its maxillae, while masticating it with the inner teeth of the mandibles (fig. 4). In this way a food bolus as typical for cicindelines is formed, which is mixed with digestive fluids and macerated until a tight bolus of small, inedible particles finally remains (fig. 5) and is discarded. During this feeding *Manticora* generally stands still, although it will run for a short distance if disturbed, without letting go of its prey.
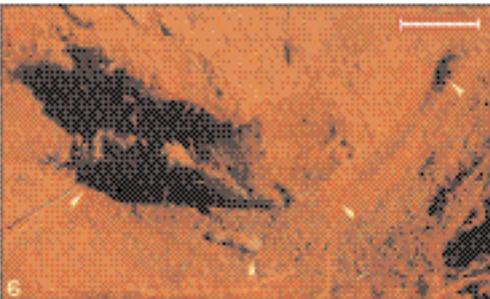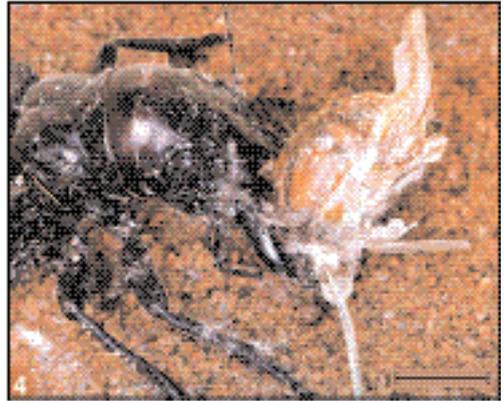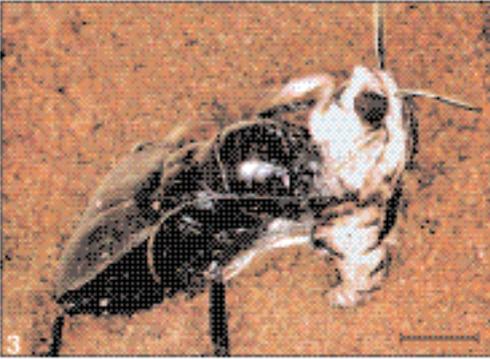
After feeding, *Manticora* wipes its mandibles clean by biting into the sand several times. The antennae are carefully cleaned by pulling them through the protibial cleaners a number of times, and the beetle may also wipe its head and eyes with its front legs.

In captivity at least, feeding beetles were often disturbed by other individuals excited by the scent of the prey. Such a beetle would pounce on the feeding specimen just as it would on the prey itself, in its frenzy evidently not being able to immediately distinguish the latter from the hunter. Its bite would never hurt the feeding beetle, and usually at that stage it would seemingly realize that the prey was already 'spoken for' and give up its attack. The feeding beetle would also only turn away slightly from the attacker, never run. Only on rare occasions involving a large prey item still struggling in the mandibles of one beetle would another seize it as well and sometimes pry away a piece of it. Food stealing more frequently involved picking up severed pieces of prey from the ground where these had fallen from the mandibles of a feeding beetle.

Females are considerably more effective in seizing prey than are the males with their huge, curved mandibles. Especially with prey items of the size of termites or globose, smooth melolonthine beetles, the male's bite often closes above the prey as the mandibles hit the ground, and the beetle has to crouch lower, lift its head and bite forwards, rather than downwards as it usually does. It is clear that the male's enlarged mandibles are more of a hindrance than an aid in catching prey. They have a secondary function in mating behaviour.

Mating and oviposition

Male *Manticora* detect females also by smell and, on doing so, display a behaviour similar to that of hunting prey. They rapidly zigzag along the scent trail and pounce on the female just as they would on a prey. The mandibles, however, are clasped around the base of the female's prothorax, where they fit into lateral coupling grooves and the curved apices close underneath the female in a strong grip that she is seemingly unable to escape. In this mandibular amplexus the males rides on the female for a considerable length of time (up to an hour observed in captivity), his front and sometimes also middle legs off the ground. The female generally stands still during such am-

plexus, even continuing feeding if she was doing so before. Occasionally she would attempt to dislodge the male by running and ducking under some obstacle, upon which he would sometimes let go but often persevered in the amplexus and prevented her from dislodging him.

The male usually attempts copulation immediately after clasping the female, by inserting the tip of his aedeagus between the tergite and sternite of her apical abdominal segment. Whether such copulation always leads to successful mating is unclear; however, the female seems unable to resist it. Copulation usually lasts about 5-10 minutes, after which the male withdraws the aedeagus but remains in amplexus. He may copulate several times while riding on the female.

Sometimes a hunting male encounters a female feeding on a freshly killed prey. It is unclear whether he already detects this by smell before he comes upon it; however, in all such observations the male inevitably went into amplexus on the female and copulated with her. Mating pairs are also often intruded on by other males, the newcomer grasping the riding male with its mandibles either in an attempt to throw him off or, apparently more commonly, to mount on top of the mating pair and seize the riding male in an amplexus. The newcomer then tries to copulate with the female; however, the strongly convex abdomen of the male beneath him makes this almost impossible. In addition, the first male will insert his aedeagus into the female's genital opening so as to block it off. With this action and his mandibular amplexus he is able to guard the female effectively against mating attempts by other males. Only if the male is rather small (and thus, too, his mandibles) does a larger male sometimes succeed in throwing him off and mounting the female; this appears to result more from the squeeze of the larger male's bite rather than by him breaking the smaller male's mandibular amplexus.

Péringuey (1893) noted that males are 'very pugnacious among themselves'. Indeed, they often pounce on one another as if seizing a prey or a female, but this was never observed to result in an outright and prolonged fight. It is more aptly described as a quick 'skirmish by accident' until the combatants realize that the opponent is neither an edible prey item nor a receptive female, upon which they will break their grip and go their separate ways. The large mandibles are evidently not used as weapons in male fights over females or oviposition sites.

On three occasions it was possible to keep individuals from the Lapalala (*M. latipennis*) and Pretoria (*M. mygaloides*) populations together in captivity. Interaction between the beetles was no different than between those of the same population, the smaller *M. mygaloides* males copulating with the larger *M. latipennis* females and *vice versa*. The smaller *M. mygaloides* beetles also generally had no problem defending their food bolus from the larger *M. latipennis*, although the *M. mygaloides* males were at a noticeable disadvantage when in amplexus on a larger *M. latipennis* female and a *M. latipennis* male attempted to dislodge them. These were the only occasions witnessed when a second male succeeded in displacing a male in amplexus and copulation (except when the first male had already been in amplexus for a considerable time and was about to dismount in any case).

Oviposition was observed in the field only once, when a few females were seen laying eggs in the shoulders of a gravel road at Pniel near Barkly West. In captivity later, the female taken laid eggs in a similar fashion in the terrarium. To do so she pushed the pointed tip of her abdomen a short distance into the soil, raising her forequarters up on her front legs, and inserted her ovipositor deeper into the ground. A single egg was laid in each such hole; the eggs excavated were found to have been placed in a slight cavity at a depth of about 20 mm. *M. latipennis* females from Lapalala were only seen to oviposit once in captivity, despite many years of keeping this species; presumably the soil and perhaps also other conditions in captivity were not conducive for this. No larvae of this species emerged in captivity. From larval tunnels found in its habitat, it seems that the shoulders of reinforced gravel roads also present ideal conditions for oviposition and larval development in *M. latipennis*.

The incubation time of the eggs is uncertain. The captive female from Pniel was observed ovipositing intermittently from December 1984 to January 1985. However, two first-instar larvae only appeared in the container in April 1986, and it was not possible to ascertain how long before the eggs were laid.

Figs. 1-7. Biological aspects of *Manticora* Fabricius. – 1, Head of male *M. mygaloides* Thomson in alert hunting posture, with antennae held out from body and mandibles half agape (Barkly West, December 1984); 2, same specimen pausing with a quivering motion of the body; 3, male *M. latipennis* Waterhouse killing large prey (sphingid moth) with crushing bite (Lapalala, February 1991); 4, same specimen masticating prey into food bolus; 5, male *M. mygaloides* in final stage of masticating food bolus (grasshopper) just before discarding unpalatable remains (Barkly West, December 1984); 6, early third-instar larva of *M. mygaloides* next to excavated tunnel (Pretoria, December 1992), arrows f.r.t.l. indicating tunnel entrance, bend, excavated larva and bottom of tunnel; 7, mature third-instar larva of *M. latipennis* in tunnel entrance (Pretoria, March 1991). Scale bars 10 mm for figs 1 – 5, 100 mm for 6, 20 mm for 7.

Sheltering and hibernation

In the wild, *Manticora* was observed retreating to existing shallow shelters in the soil and also digging these in the late afternoon. A beetle would usually select a secluded spot under a stone, piece of wood or grass tuft for this purpose, but was also seen digging a hole in the open on the shoulder of a road. The earth is loosened with the mandibles and then pushed backwards with the legs, and in the sandy soil of their habitats this process is rather quick. Freshly dug holes were found to extend for only about twice the body length of the beetle, which rests at the end of the cavity with its head and mandibles facing towards the entrance. The mouth of this seemingly temporary shelter is generally left open, and in the morning or afternoon the beetle simply leaves it.

In captivity, the beetles dug deeper and more permanent holes, starting under a stone and extending the tunnel in a gently slanting fashion for about 300 mm, mostly with a fairly sharp bend occurring about 100 mm from the mouth. Such tunnels were constructed over several nights, the beetle digging a little further every evening. In the confined space of the containers, these burrows were often shared by two or even three beetles, of the same or different sexes, the first beetle retreating to the bottom and the other staying near the entrance well apart from the first. They would not fight over such burrows. If a burrow was too shallow to accommodate more than one beetle, the original occupant would defend it and the intruder leave immediately, but if it was deep enough, the original beetle would simply retreat deeper into it and leave the entrance area to the intruder.

To these burrows *Manticora* would retreat every night, generally staying near the entrance at first but retreating deeper into the soil as the temperature dropped towards morning. They also sheltered in these burrows during the heat of the day, again selecting the depth according to the temperature. The entrance played an additional role in the beetles' thermoregulatory behaviour in that here they would catch the early-morning or late-afternoon sun to warm themselves when emerging from the cooler depths of the burrow. Under inclement conditions, mostly prolonged droughts but seemingly also during shortage of food, the beetles closed off the entrances with soil and stayed in the burrows for a period, appearing again when the soil was wetted by rain. When they appeared on the surface, they generally first searched for free water or very wet sand to drink, biting deep into the sand with their mandibles and imbibing water with their mouthparts for up to 10 minutes. After that they would preen themselves and clean their antennae, before setting off to find food.

At the end of summer, the beetles close their burrows thoroughly and dig even deeper into the soil, where they hibernate until the following spring or summer, emerging only after thorough rains have penetrated the soil to the depth of their burrows. In hibernation, the beetles enter a state of decreased metabolism, almost stupor, and are largely immobile and uncoordinated when dug up.

Some beetles repeated this cycle three or even four times in captivity, most of them eventually dying during hibernation or shortly after emerging from it. Since the precise adult life span is not known, it is unclear whether they had simply aged or whether the conditions of captivity (particularly in winter) exerted unnatural stress on them and ended their life prematurely. However, it is evident that hibernation and the accompanying prolonged abstinence from feeding is the physiologically most critical phase of their lives and may account for most of their mortality other than from predation.

Prey spectrum

It is notoriously difficult to observe prey catching behaviour by *Manticora* under field conditions and thus establish the identity of its natural prey (Péringuey 1893, Horn 1910, Roer 1984). In our observations this was also only achieved on three occasions. In February 1977 a specimen of *M. mygaloides* (*livingstoni*) was found feeding on a common cricket (*Gryllus* sp., Gryllidae), in February 1991 a female of *M. latipennis* was seen feeding on the remains of a grasshopper nymph, and in December 1992 a male *M. mygaloides* was encountered feeding on a mature larva of *Cirina forda* (Saturniidae) under the *Burkea* tree these caterpillars had almost defoliated. All other information on the prey spectrum of *Manticora* stems from observations in captivity, where the beetles were exposed artificially to different prey species, including some that they may only rarely or never encounter in their habitats (see also Roer 1984, and below).

In the senior author's experiments involving captive beetles from the populations at Pniel, Lapalala and Pretoria, insects of various orders as well as other invertebrates were offered to the beetles. The following items did not elicit hunting and feeding behaviour in *Manticora*: lizards and scorpions (in agreement with Roer 1984), spiders (Lycosidae), ticks, millipedes and snails. Woodlice (Isopoda : Porcellionidae) were not readily identified as prey but sometimes seized and eaten when at close range and the beetles were hungry. The following insects, however, were consistently recognized as prey and readily eaten, although the intensity of the response their presence evoked in *Manticora* varied: crickets, mole crickets, grasshoppers and locusts, termites, cockroaches, melolonthine and ruteline Scarabaeidae and their larvae, mealworms (Tenebrionidae), various moths and caterpillars, and fly larvae. Cockroaches, caterpillars

and most other beetle larvae elicited only moderate response from *Manticora* in that they were generally not hunted (i.e. their trail not followed), although the beetles would seize and eat them readily when detecting them at close range. Moths (even large ones such as *Agrius convolvuli*, figs 3, 4) were more readily seized and eaten when found resting on the ground or on low vegetation, such as under a light in the morning, even though the numerous scales clearly troubled the beetles. Hard beetles such as native Tenebrionidae (genera *Psammodes, Phanerotomea, Dichtha, Zophosis*) were also recognized as food and seized, but *Manticora* could never crush these and always released them after a few attempts.

The strongest feeding response in *Manticora* was undoubtedly elicited by crickets, grasshoppers, termites and melolonthine beetles. When such an insect was dropped or fell into a terrarium with a number of hungry *Manticora*, a frantic scramble would follow, with all beetles rushing around and biting at everything they encountered, including their own kind. Termites and small melolonthines were seized and masticated without great trouble (unless they dug into the soil, where *Manticora* would not follow), but the fast crickets and grasshoppers often managed to outmanoeuvre the beetles for a while until they were driven into a corner of the container and then seized and overpowered in a fast attack. It is evident that these insects constitute prey items also in the natural habitats of *Manticora*.

Behaviour of the larva

Activity pattern

In the natural habitats of *Manticora*, open larval burrows were found only during summer, i.e. the period from November to March. Burrows of all three larval instars always occurred together in an area, indicating that oviposition probably takes place throughout summer, that particular developmental stages are not linked to specific times of the year, and that the entire phase of larval development spans at least a year.

The circadian activity rhythm of the larvae (both in habitat and captivity) is similar to that of the adults, in that the larvae also lie in ambush for prey at their tunnel entrance early in the mornings and late in the afternoons, but retreat deeper into the tunnels at noon and at night. During such times the tunnel entrance is left open, but when weather conditions become inclement, such as very hot and dry or cold and very wet, the larva closes the tunnel entrance for varying lengths of time. The burrow is also sealed during winter when the larva hibernates, and while it moults to another instar and presumably also at pupation and during the pupal stage.
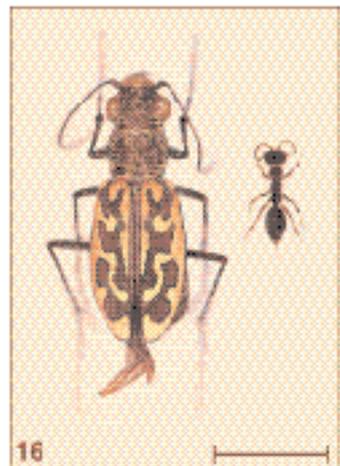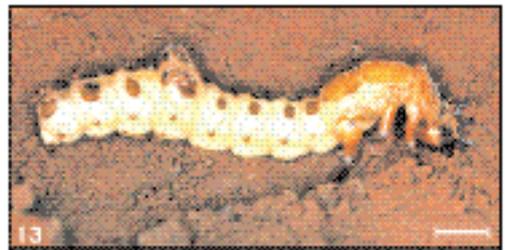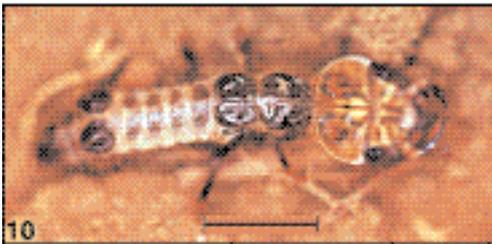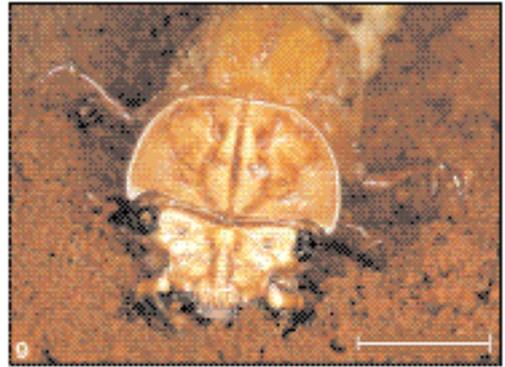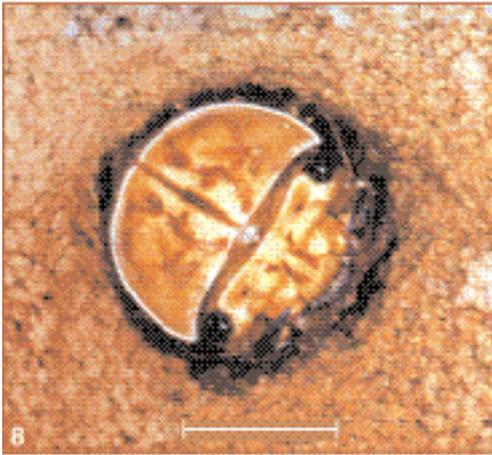
Tunnel construction

Like other cicindeline larvae, that of *Manticora* also digs its burrow with its mandibles, using its head and pronotum to move loosened soil to the entrance and then flick it away backwards over often considerable distances, up to 400 mm in fully grown larvae of *M. latipennis* (Oberprieler & Grobbelaar 1991). In captivity at least, the soil was usually flicked in the same direction, resulting in the formation of a shallow heap to one side of the tunnel entrance. This pile of soil however disintegrated rapidly, so that the tunnel entrance was invariably level with the surface of the ground and situated on a bare patch of soil. The edge of the entrance is generally somehow hardened, which prevents it from crumbling, and the larva is meticulous in keeping its burrow clean and free from loose soil. Digging and general tunnel maintenance takes place during the night, when the periodical flicking of soil from the entrance is less noticeable than it would be during the day.

The entrance hole of the tunnel is circular as in other cicindelines and corresponds with the head-pronotum diameter of its occupant (fig. 8), varying between instars and also between species. Holes of the first instar have a diameter of about 4-7 mm, of the second instar 8-10 mm, and of the final instar 12-16 mm.

The shape of the tunnel is different from those of all other known cicindeline larvae in that it is not vertical and straight but turns in both the horizontal and the vertical planes, often extending to considerable depths. The length and depth vary with the soil moisture of the area, the deepest burrows being found in the comparatively driest localities, and probably also depend on the type and density of the soil. The shapes of the burrows found in our investigations varied among individual larvae of a colony, especially in the last instar, but showed a noticeably greater complexity in *M. latipennis* (Tshipise, Lapalala) than in *M. mygaloides* (Pretoria, Waterberg Namibia).

In the Pretoria population of *M. mygaloides*, the excavated tunnels of the final larval instar were relatively simple in that they sloped at a steady angle in a more-or-less straight fashion for just over a third of their length (ca 200 mm), then turned in a broad spiral segment of about 150 mm length into the final, again straight and gently descending part of about the same length (fig. 6), reaching a total length of about 500 mm with a depth of 300 mm. The burrows of *M. mygaloides* from the Waterberg population in Namibia similarly did not turn horizontally at the entrance but were quite variable in shape, extending to about 190-300 mm in depth and 380-600 mm in length (slightly shorter in the first and second instars).

By contrast, in *M. latipennis* the larval burrow turns into a nearly horizontal tunnel almost at the en-

trance, leaving just a portion of about the larva's body length curving into the vertical (fig. 7). After about 70 mm in the horizontal, the tunnel continues in an obliquely downward direction for another 350 mm before ending in a short vertical part. Generally the burrow also turns sidewards after about half its length, so that its overall shape is that of a large spiral turning about one full circle (see also Oberprieler & Grobbelaar 1991). In the Tshipise population, the burrows of the last instars were about 400-500 mm long and 300 mm deep, while those of the Lapalala population extended to depths of almost 1 m (Oberprieler & Grobbelaar 1991), perhaps due to the soil conditions of the road shoulders in which they were located. The burrows of the second and first larval instars are only slightly shorter than that of the last.

Prey detection, capture and feeding

Like the larvae of other Cicindelinae, the *Manticora* larva also lies in wait for its prey at the tunnel entrance, where the mottled colour pattern of its head and pronotum blends in well with the surrounding soil (fig. 8). The larva has excellent vision, its beady eyes (figs 8, 9) used both for detecting potential enemies (which causes the larva to rapidly retreat down its burrow) and for spotting likely prey items from a considerable distance. It appears that the larva detects prey movement rather than distinctive shapes, but that the latter and also very slow movements may be detected against a light background, such as the skyline, but not against similarly coloured and shaped objects nearby. However, the larva is obviously able to recognize size because it ignores items too big to be dragged down its burrow, and it is evidently also able to distinguish between palatable and unpalatable prey, as it would ignore strongly sclerotized beetles but take crickets of similar size and shape. Possibly the difference in movement (both speed and continuity) between these two types is a cue for the larva in recognizing suitable prey.

Usually the larva remains motionless when it has detected an approaching prey, but sometimes it will stealthily turn around so that its mandibles face away from the prey. When the prey has come into striking distance (about two-thirds of the body length of the

larva), the larva lunges out of its burrow in a lightning-fast, backward strike, seizes the prey in its sharp mandibles and draws it down into the burrow. Occasionally larger prey items resist being pulled down for a while; the *Manticora* larva then maintains its grip and continues to pull until the prey succumbs to its digestive juices and can be dragged down. Smaller and slower prey items are sometimes also seized with a sideways movement of the head, or even picked up from the front of the head by the mandibles, but only when they are very close to the tunnel entrance. Larger and faster prey approaching from the front is generally ignored by the larva, even when at the tunnel entrance, but is sometimes seized from the rear as it departs and comes into range of the backward lunge of the larva. This clearly constitutes the main capture technique.

The success rate of the lunging larva is remarkably high, only two instances of it failing to seize the prey having been observed. One of these involved a large sarcophagid fly, which had landed and was moving near the tunnel entrance; its take-off was even quicker than the lunge of the *Manticora* larva. The other involved an obviously alert grasshopper poised to jump and already facing away from the tunnel; again the *Manticora* larva was too slow and the grasshopper far away and quick enough to jump away from the larva. Usually, however, the larva is patient enough to wait for the prey to come well within reach of its mandibles and will only seize upon slight movements of the prey. Grasshoppers generally had no chance of escaping the attack of the larva, and on another similar occasion involving a large fly, the larva succeeded in seizing it.

After feeding, the larva discards the inedible remains of the prey by flicking them away from the tunnel entrance. This, however, did not always happen before the larva commenced ambushing another prey item, particularly when abundant prey such as swarming termites was around. In such circumstances the larva would catch several prey items in quick succession and drag them into the burrow, evidently without feeding on them straight away. Presumably it would do so immediately after the swarming was over, rather than caching prey for extended periods of time, but this requires further investigation.

Figs. 8-16. Biological aspects of *Manticora* Fabricius (cont.). – 8, Mature third-instar larva of *M. latipennis* in ambush position in tunnel entrance (Lapalala, February 1991); 9, mature third-instar larva of *M. latipennis,* head and pronotum, frontal view (Lapalala, February 1991); 10, first-instar larva of *M. mygaloides,* dorsal view (Pretoria, December 1992); 11, early third-instar larva of *M. mygaloides,* dorsal view (Pretoria, December 1992); 12, mature third-instar larva of *M. latipennis,* dorsal view (Lapalala, February 1991); 13, same specimen, lateral view; 14, undescribed *Methocha* species (Tiphiidae) (South Africa, Kruger National Park, Shirombe Pan, 24.i.1984, C. Eardley; SANC); 15, same specimen in size comparison with male *M. latipennis* Waterhouse, its suspected host; 16, *Methocha minima* André (Lesotho, Mamathes, 8.x.1944, A. Jacot-Guillarmod; SANC) in size comparison with *Lophyra neglecta* (Dejean), one of its likely hosts. Scale bars 10 mm except 5 mm for figs 10, 14 and 16.
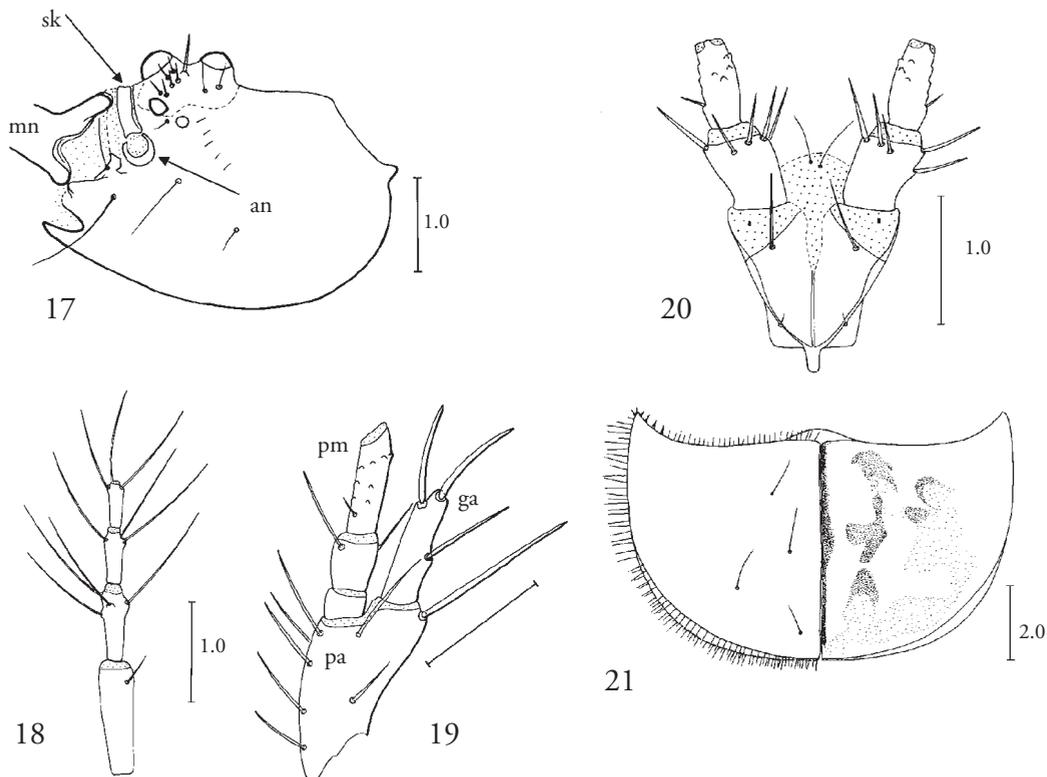
Figs 17-24. Morphological details of larva of *Manticora latipennis* Waterhouse. – 17, L$_1$ head, lateral view (an - antennal base, mn - base of mandible, sk - sclerotized keel); 18, L$_1$ antenna, left side, dorsal view; 19, L$_1$ maxillary palpus and galea, left side, dorsal view (ga - galeomere II, pa - palpifer fused with galeomere I, pm - palpus maxillaris); 20, L$_1$ labium, ventral view; 21, L$_1$ pronotum, dorsal view; 22, L$_1$ tergite V, left half, dorsal view; 23, L$_3$ tergite V, left half, dorsal view schematic (ap - anterior part, ih - inner hook, lp - lateral part, mh - median hook, pp - posterior part); 24, L$_1$ sclerites of abdominal segment III, left side (ep - epipleurite, hy - hypopleurite, ls - laterosternite = coxal lobe, st - sternite, te - tergite). All scales in mm.

Prey spectrum

No prey capture by *Manticora* larvae under field conditions has yet been recorded, and all observations on the prey spectrum reported here are based on trials in captivity. Mature larvae fed on almost the same prey spectrum as the adult beetles, namely crickets, mole crickets, grasshoppers and locusts, termites, cockroaches, melolonthine and ruteline Scarabaeidae and their larvae, mealworms (Tenebrionidae) and some moths and caterpillars. Snails and millipedes were again ignored by the larvae, possibly because of their slow movement and large size. Smaller larvae also accepted termites, immature crickets and grasshoppers as well as small cockroaches, melolonthines, mealworms and caterpillars. They also readily took woodlice and sometimes large ants such as *Camponotus*; the latter, however, were often seized and dragged into the burrow but ejected again shortly afterwards.

From these observations as well as extrapolations from the insect fauna of their natural habitats it appears that the natural prey spectrum of the larvae consists mainly of terrestrial phytophagous insects such as termites, grasshoppers, crickets and certain beetles and caterpillars.

Natural enemies

No records of *Manticora* larvae being preyed upon or parasitized are available, and the identity of any natural enemies is thus unknown. However, a large (18 mm long) black *Methocha* wasp has been collected in the northern Kruger National Park in South Africa (fig. 14), within the distribution range of *M. latipennis*, and since this genus of Tiphiidae is constituted of specialized parasitoids of tiger beetle larvae (Pearson 1988) and the undescribed species is of the same size ratio to *Manticora* (fig. 15) as the smaller species of
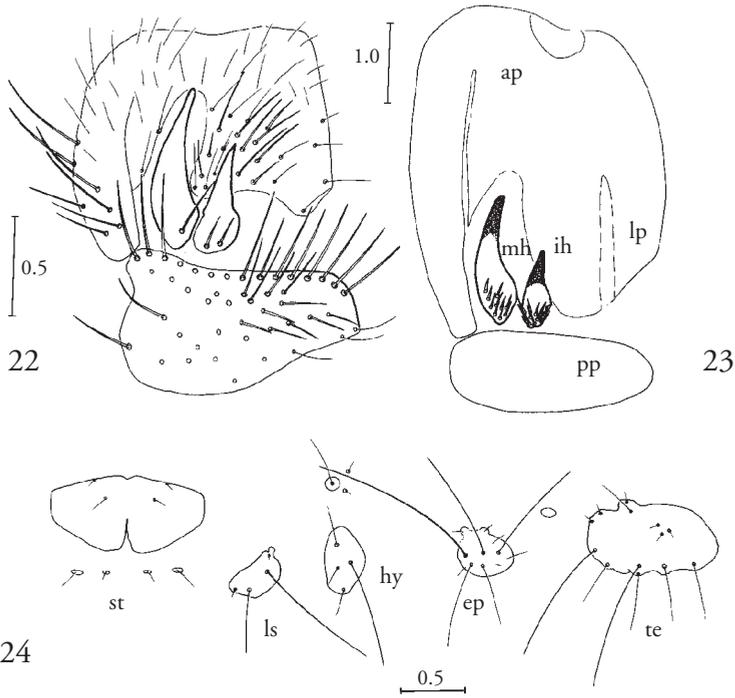
Methocha in southern Africa are to their presumed hosts (fig. 16), it is likely that this giant *Methocha* is a parasitoid specific to *Manticora*. The likely process of parasitization of *Manticora* larvae by this wasp was sketched by Oberprieler & Grobbelaar (1991), following the general behaviour and biology of these wasps (Burdick & Wasbauer 1959). The precise nature of this hypothesized association between *Manticora* and this large *Methocha* is nevertheless in need of verification and detailed investigation, as are those of other possible hymenopteran or dipteran parasitoids.

Description of the larva

Instar I (fig. 10)

Habitus and coloration: Larva very large (measurements in table 1). Dorsal side of head and pronotum yellowish with brown pattern; stemmata region dark brown; meso- and metanotum, legs, sternites and pygopod yellow; ventral side of head, head appendages and tergites as well as setae brown. No metallic lustre.

Microsculpture: Head, pro-, meso- and metanotum with fine isodiametric mesh pattern, legs less distinctly so, sternites and tergites with meshed to pointed microsculpture, head appendages without regular microsculpture.

Head: 4 stemmata present, 2 very large; region of stemmata protruding; a sclerotized keel between stemma II and mandibular base (fig. 17), this keel continued less distinctly on lateral part of head. Frontale multisetose, setae of frontale short; U-shaped keel in posterior part of frontale joining the keel on posterior part of vertex; keel protruding, covered with a row of setae on parietale, mostly with 1 seta on frontale region but this seta absent in some specimens. Posterior part of frontale with egg bursters consisting of 2-4 small teeth. Coronal suture very short, posterior margin of head capsule arched mesally, nearly extending to posterior point of frontale. Nasale protruding, anterior margin wave-shaped, distinctly separated from adnasale by two deep trapezoid foveae. Mandible slender, apical part about as long as basal including retinaculum, with several stout setae basally and laterally; dorsally with two sharp edges. Antenna inserted anterioventrally of eyes, separated from mandibular base by a slender sclerotized bar. Antenna (fig. 18) thin and short, much shorter than apical part of mandible, with antennomere I largest and antennomere IV smallest; antennomere I slightly thicker than the others, with 1 seta dorsoapically, antennomere II with 4 large setae apically, antennomere III with 3 long setae, sensorial appendage absent but replaced by small field of pores, antennomere IV with 3 setae subapically. Maxilla with divided cardo, dorsal

Table 1. Measurements of examined *Manticora* larvae (all data in mm, averages in parentheses)

Species, instars, number of examined specimens	Head width	Frontal width	Pronotal width	Pronotal length
M. tuberculata (*tibialis*)				
L1 (n=1)	3.2	1.9	3.2	2.1
L_2 (n=2)	4.6, 4.8	2.9, 3.1	5.1, 5.3	3.0, 3.1
L_3 (n=2)	7.6, 7.8	4.6, 5.0	8.4, 8.6	4.8, 5.2
M. latipennis				
L_1 (n=4)	4.2-4.4 (4.3)	2.6-2.8 (2.7)	4.4-4.7 (4.6)	2.8-2.9 (2.9)
L_2 (n=4)	6.1-7.2 (6.7)	3.7-4.2 (4.0)	6.4-7.4 (7.0)	4.0-4.7 (4.4)
L_3 (n=3)	9.4-11.0 (10.1)	5.8-6.8 (6.3)	10.8-12.4 (11.5)	6.4-7.2 (6.8)
M. mygaloides				
L_1 (n=1)	4.3	2.6	4.5	2.8
L_2 (n=1)	7.5	4.7	8.2	4.7
L_3 (n=1)	10.0	6.2	11.2	6.4
*M. mygaloide*s (*livingstoni*)				
L_1 (n=5)	4.1-4.3 (4.2)	2.5-2.6 (2.6)	4.4-4.6 (4.5)	2.4-2.8 (2.6)
L_2 (n=2)	6.1, 6.2	3.8, 4.0	6.9, 7.0	3.8, 3.9
L_3 (n=2)	10.0, 10.4	6.0	11.0, 11.2	6.4, 6.6

part in form of a slender bar, ventral part triangular; stipes of typical cicindeline shape, about 2.5-2.7 times longer than wide, with 1 spine mesobasally, membranous field dorsally restricted to laterobasal area, laterally multisetose with extended setal field gMX comprised of about 80 setae, ventrally nearly without setae; lacinia absent; a strongly sclerotized bar with 3 setae between stipes and palpifer; palpifer (fig. 19) large, completely fused with galeomere I dorsally and ventrally; palpifer with 4 long setae laterally, 2 setae dorsally, 1 smaller seta ventrally; galeomere I with 1 large stout seta mesoapically; galeomere II (fig. 19) large with 3 stout setae, 2 of them large and apically inserted; maxillary palpus (fig. 19) including palpifer longer than galea; maxillary palpus (excl. palpifer) 3-segmented, palpomere I small without setae; palpomere II about 2 times longer with 1 large seta each dorsally and ventrally; palpomere III longest, about 3.6 times longer than palpomere I, with 1 small seta dorsobasally and with nap-shaped structures and large and wide apical sensorial field turned outwards, elongate sensorial fields absent. Prementum ventrally distinct, triangular, dorsally covered by an extremely bulging multisetose hypopharynx; ligula flat, not distinct, with 1 pair of setae; prementum ventrally with 1 long and 1 short seta; ventral double sclerite absent between prementum and palpomere I, only a sclerotized tip present (fig. 20). Labial palpomeres of subequal length, palpomere I with apical ring of 5 setae, palpomere II with 1 seta laterally and with nap-shaped structures but without elongate sensilla; apical sensorial field wide, turned

slightly outwards. On ventral side of head gular suture complete, V-shaped.

Thorax: Pronotum with distinct postero-lateral edge, disc with only 4 primary setae per half and with flat, indistinctly relief-like structure (fig. 21) and characteristic dark pattern (figs 8-11). Meso- and metanotum multisetose, mesonotum with dense field of setae along median suture. Legs with elongate femur, long and wide tibia bearing ventrally and laterally a field with dense setae, and smaller ventrally multisetose tarsus. Two claws, anterior claw sabre-shaped, 2-3 times longer than posterior one; basally a very small separate sclerite with short seta.

Abdomen: Tergite I with 8 long and 8-10 short setae; tergites II-IV with 8 long and 6 short setae. Epipleurite consisting of 1 large sclerite with about 5 long and 5 short setae; hypopleurite consisting of 1 large and 2-3 small sclerites, large sclerite with 3 long and 1 short setae, small sclerites with 1 seta each, length of setae variable. Coxal lobe with 3-4 setae, inner sternite with 2 short setae, posterior sternites indistinct, consisting of 2 pairs of small sclerites each with 1 seta (fig. 24). Tergite V protruding, consisting of only 2 parts, lateral and anterior part of tergite fused, suture visible as small groove; all tergal parts multisetose. Two short, drop-shaped hooks on each side, outer hook with 1 long seta basally, inner hook with 2 shorter setae basally (fig. 22). Pygopod multisetose.

Instars II and III
(figs 7-9, 11-13, measurements in table 1)
The following character states are different from

Table 2. Morphological differences between larvae of examined species of *Manticora*.

Character	M. tuberculata (tibialis)	M. latipennis	M. mygaloides	M. mygaloides (livingstoni)
Length of seta FR_3 on frontale (all instars)	distinctly longer than remaining setae on frontal disc	very short, not distinguished from remaining setae on frontal disc	very short, not distinguished from remaining setae frontal disc	very short, not distinguished from remaining setae on frontal disc
Number of setae on galeomere II (L_3)	4	6-7	6-7	6-7
Pubescence of mesonotum (L_2 and L_3)	glabrous areas on disc larger than pubescent areas	glabrous areas on disc larger than pubescent areas	mesonotum nearly completely pubescent; glabrous areas very restricted	mesonotum nearly completely pubescent; glabrous areas very restricted
Pubescence of metanotum (L_2 and L_3)	pubescent area restricted to anterior margin	pubescent area restricted to anterior margin	pubescent area covering anterior half	pubescent area covering anterior half
Number of setae on ventral side of head (L_2 and L_3)	less than 30 per half	less than 30 per half	about 30 per half	more than 40 per half
Arrangement of setae in ventrobasal region of stipes (L_2 and L_3)	not arranged in row	not arranged in row	not arranged in row	arranged in one simple row

the first instar:

Head: Egg bursters in L_2 less distinct, in L_3 absent. More setae present on most sclerites, e.g. on frontale in the region of posterior ridge of parietale; antennomere I with 7-9 setae, antennomere II with 6-9, antennomere III and IV like in L_1. Labial palpomere I multisetose, galeomere I with 4-5 stout setae in L_2, 6 in L_3, galeomere II with 5-6 stout setae in L_2, 4 or 6-7 in L_3. Maxillary palpomere I with 1 large seta on outer margin as in palpomere II. Mesobasal side of stipes only with 1 hook as in L_1. Sharp teeth on outer margin of mandible more developed than in L_1.

Abdomen: Many more setae on all sclerites, except on sternites. Setae also in membranous regions between sclerites. Hooks (fig. 23) with variable number of short, stout setae, outer hook with at least 6 in L_2 and 7 in L_3 (maximally 16 recognized in *M. latipennis* and 19 in *M. mygaloides*); inner hook with at least 7 in L_2 and 9 in L_3 (maximally 14 recognized in *M. latipennis*).

Distinguishing features

The larvae of *Manticora* are distinguished from those of all other cicindelines by a number of unique characters. The following character states of *Manticora* are autapomorphic: four stemmata; ocular region protruding; sclerotized bar present between stemma II and mandibular base; antenna inserted anteroventrally of eyes, separated from mandibular base by slender sclerotized region; antenna thin and short, much shorter than apical part of mandible; palpifer large, completely fused with galeomere I dorsally and ventrally; terminal articles of both palpi with nap-shaped structures and large and wide apical sensorial field turned outwards; frontale with deep foveae between nasale and adnasale region; tibia long and wide, ventrally and laterally with field of dense setae; tergite V protruding, consisting of only two parts, lateral and anterior part of tergite fused, basal part of both hooks with numerous setae. Four features as described by Leffler (1980) - three stemmata present; claws of posterior legs subequal; hypopleurite consisting of several small sclerites; hooks of abdominal tergite V without setae - could not be confirmed with our material and are probably incorrect.

The larvae of the populations examined are comparatively varied, but a number of seemingly consistent differences are evident (table 2). *M. tuberculata (tibialis)* is distinguishable from the other taxa by two constant characters of the chaetotaxy, and two similar characters serve to distinguish *M. latipennis* and *M. mygaloides*. The larva of *M. mygaloides (livingstoni)* has two additional unique features, but their consistency and taxonomic significance is as yet unclear.

DISCUSSION

Mandibular adaptations

The lack of observations on prey-catching behaviour by *Manticora* in the field and a comparison of the size of its head and mandibles with those of physically similarly, snail-shell breaking carabids led Thiele (1977) and Roer (1984) to propose that *Manticora* is also adapted for hunting large and strongly sclerotized prey. Thiele (1977) suggested large scorpions as the likely main prey, and Roer (1984) set up an experiment in captivity to demonstrate such a 'procerization' type of hunting adaptation in *Manticora*. He exposed three starved captive beetles from Okahandja (identified as *M. latipennis* but representing *M. mygaloides,* see below) at the Namib Desert Research Station of Gobabeb to a number of animals occurring in the Namib dunes, namely the lizard *Aporosaura* (*A. anchietae* (Bocage), Lacertidae), the 'Namib' scorpion *Opisthophthalmus* (probably *O. flavescens* Purcell, Scorpionidae) and three species of *Onymacris* beetles (Tenebrionidae). In this experiment, the lizard and the scorpion elicited no prey catching behaviour in *Manticora*, whereas the tenebrionids did so readily. Of these, however, *Manticora* could not crush the more heavily sclerotized *O. plana* (Péringuey) and *O. rugatipennis* (Haag), only the weaker *O. laeviceps* Gebien. Since the last-named species does not occur in the natural habitat of *M. mygaloides*, Roer (1984) speculated that other Tenebrionidae in its habitat around Okahandja, such as the genera *Gonopus, Himatismus* and *Eurychora,* as well as scarabaeids (*Copris*) and carabids (*Calosoma*), were likely to constitute natural prey items of *Manticora*. This is mostly improbable though, as *Gonopus* and *Eurychora* are also heavily sclerotized, *Himatismus* are arboreal and nocturnal beetles and generally out of reach for *Manticora*, and *Calosoma* (more correctly: *Caminara*) are active and chemically protected predators themselves. Of this list, only dung beetles such as *Copris* are feasible prey items of *Manticora*, but whether they are indeed hunted and constitute significant prey items remains to be demonstrated. While Roer (1984) could refute the scorpion-specialist hypothesis of Thiele (1977), he perpetuated the snail-shell breaker notion despite the clear implications of his own experiments with *Onymacris*. In addition, both he and Thiele (1977) failed to appreciate the significance of the sexually dimorphic development of the mandibles of *Manticora*.

Although the prey spectrum of adult *Manticora* in its natural habitats is still largely unknown, the observations and experiments presented here show that these tiger beetles are not specially adapted to feeding on strongly sclerotized prey, but that they are opportunistic hunters that feed on almost all types of insects (but not arachnids) they can find and overcome. Rather than being adapted for breaking hard shells and exoskeletons, their large head and mandibles are more suited to seizing large, fast and evasive prey, which is tracked by smell and overpowered in a surprise attack. From our observations, and considering the common diurnal insect fauna in the sandy, terrestrial habitats of these beetles, it seems that their main prey items consist of medium-sized to large, flightless but agile phytophagous insects such as grasshoppers, locust hoppers, crickets, termites, certain scarabaeids and other beetles, and some types of caterpillars. Their larvae apparently utilize more or less the same prey spectrum. Indeed, *Manticora* may well be a major predator of periodically swarming insects such as locusts, termites and certain caterpillars ('army worms', *Spodoptera* species, Noctuidae).

The pronounced sexual dimorphism of the mandibles of *Manticora* indicates that in the male they serve a purpose additional to food capture. Their function during copulation is evident from the prolonged mandibular amplexus in which the male rides on the female, and our observations indicate that his enlarged mandibles play an important part in guarding the female against other males and perhaps also in preventing her from unseating him. In this circumstance, a strong development of the mandibles in the male would be an obvious advantage and under selection pressure for further enlargement. Further, it is notable that a disproportionate enlargement of the mandibles occurs in the largest beetles (the *M. latipennis* complex, see below) and that this development is asymmetric, affecting only the right mandible and reaching an extreme in the long, acutely bent apical pincer of *M. imperator* (Mareš 1995). The asymmetry between the two mandibles appears to represent a trade-off between prey-catching and copulatory requirements and constraints, in that having a long, incurved pincer on both mandibles would seriously compromise the prey-catching ability of the male, while a pincer on only one mandible seems sufficient to ensure a secure grip on the female. The occurrence of such a large pincer in only the largest beetles (not in the smaller *M. tuberculata* and *M. mygaloides* complexes, below) suggests that it may be a manifestation of allometric growth, as is well-known in sexually dimorphic structures in other beetles, and that it may occur in large males of many populations. However, detailed morphometric investigations of large populations of beetles are required to elucidate this phenomenon. Interestingly, a similar condition occurs in the carabid genus *Anthia*, but affecting the left mandible of the male.

Taxonomic and phylogenetic implications

The taxonomy of *Manticora* has been notoriously

difficult (Péringuey 1893, Werner & Wiesner 1994, Mareš 1995). The definition and distinction of its various species has rested almost exclusively on a few features of the males (in particular the mandibles), the females having been regarded as almost indistinguishable (Werner & Wiesner 1994). The male genitalia, too, provide no apparent taxonomically significant differences to assist in the recognition of the various species (Mareš 1995). One of the objectives of this study is to explore the taxonomic implications of our behavioural observations and study of larvae from a number of different populations and taxa.

Recent studies of newly collected material of *Manticora* by Mareš (1976, 1995) and Werner & Wiesner (1994, 1995) provide a slightly clearer picture of the characters and distribution of the various taxa described or recognized to date, although the determination keys given by these authors are, at least in part, still based on features of very limited utility, such as size and distribution range. Based largely on the shape of the mandibles and abdomen of the males, three species complexes are distinguishable in *Manticora* (see key in Mareš 1995 for details): the *M. tuberculata* complex in the south and south-west of the southern African subcontinent, the *M. mygaloides* complex in the south-centre and south-east, and the *M. latipennis* complex in the north-centre and north-east.

According to the latest taxonomic treatment (Werner & Wiesner 1994, 1995; Mareš 1995), the *M. tuberculata* complex includes the species *M. tuberculata* de Geer, *M. tibialis* Boheman, *M. sichelii* Thomson and *M. congoensis* Péringuey. The first three taxa overlap broadly in central southern Africa (Orange Free State, Botswana) according to Mareš (1995), while *M. congoensis* appears to be allopatric from these in Angola and southern Congo. The general habitat of this complex comprises hard, stony soils rather than sandy substrates. Recently *M. tuberculata* has also been recorded from eastern Namibia (Werner & Wiesner 1995). However, this record, based on a specimen found dead ('Todfund'), is dubious, as the specimen depicted (Werner & Wiesner 1995, fig. 1) does not represent *M. tuberculata* but appears to be a composite of a male head and prothorax and a female abdomen (note differences in shape, colour, sculpture and lustre) of *M. mygaloides*.

The *M. mygaloides* complex includes the taxa *mygaloides* Thomson, *damarensis* Péringuey and *livingstoni* Castelnau, which are not only very difficult to distinguish but also overlap broadly in their distribution ranges in Botswana and especially Namibia (Werner & Wiesner 1994, 1995; Mareš 1995). Its habitats are mainly sandy soils, especially the extensive red Kalahari sands of the centre of the subcontinent.

The *M. latipennis* complex includes *M. latipennis* Waterhouse (with several synonyms) in the east and north-east of the subcontinent, the rare, apparently allopatric *M. gruti* Boucard in southern Namibia, and the large *M. imperator* Mareš known from only three males from around Lake Ngami in Botswana (Mareš 1976). Its habitats are again deep sandy soils.

The main problem in identifying and delimiting natural (biological/evolutionary) species in these complexes lies in the extreme variability of a number of rather superficial morphological features, combined with an absence of clear and evidently significant differences in non-adaptive characters such as of the genitalia. This has resulted in the recognition of a number of typological entities with confusing, mosaic distribution patterns generally with large areas of sympatry. Given a) this perplexing pattern of variation in morphological traits, b) the low vagility and narrow substrate requirements of the beetles and the consequent isolation of populations (favouring the development of population characteristics), c) the apparent adaptiveness (possibly even allometry) of traditional mandibular characters, and d) the evident lack of either structural or behavioural species recognition barriers between different taxa (see above), it is highly doubtful that closely similar species coexist in sympatry. The quest for the identification of natural species in *Manticora* therefore has to involve the identification of biologically and evolutionarily meaningful species barriers.

In the absence of a thorough and comprehensive systematic revision of the genus, our studies of the biology and behaviour and of characters of the larvae allow the following taxonomic conclusions. In the *M. tuberculata* complex, the distinction of *tibialis* and *sichelii* as separate species from *M. tuberculata* is difficult to justify with the present knowledge of their true distribution and variability; at most, *tibialis* (= *sichelii*) could be regarded as an eastern form or subspecies. *Manticora congoensis* in the north-west appears to be morphologically distinct and also allopatric from *M. tuberculata* in the south (their precise geographical ranges unclear, i.e. a specimen of *M. tuberculata* recorded from Kaokoland in Namibia, Werner & Wiesner 1995), and it could well be a northern isolate now representing a separate natural species. In the *M. mygaloides* complex, the very similar and broadly sympatric (see also Mareš 1995) forms *damarensis* and *livingstoni* can hardly be accepted as distinct natural species; their distribution in Namibia (Werner & Wiesner 1994, maps 3-4) even makes it difficult to regard *livingstoni* (= *damarensis*) as a north-western form or subspecies of typical *M. mygaloides* in the south-east. Finally, in the *M. latipennis* complex *M. gruti* again appears to be a morphologically distinct, western isolate representing a distinct natural species, whereas *imperator* is more likely to represent only an extremely large, north-

western form or population of *M. latipennis.*

At present therefore, it is hard to defend the existence of more than five natural species in *Manticora*, the eight or even ten as recognized by Wiesner (1992) and Mareš (1995), respectively, representing a purely typological approach and classification system. It is apparent that only a thorough, detailed and comprehensive systematic revision of the genus will establish the real number of species and their delimitation. Such an investigation should incorporate a study of longer series of larvae from all critical populations, a morphometric analysis of all critical populations and characters, an examination of crucial demographic and ecological aspects such as vagility, population size, substrate requirements and the effect of adverse environmental factors on the size and development of morphological traits, and an exploration of the precise specific-mate-recognition systems of these beetles. Modern techniques of molecular analysis may also prove to be an extremely useful tool in investigating the taxonomy of this genus.

Finally, our examinations of the larvae of *Manticora* have some bearing on the phylogenetic position of the genus. *Manticora* and its putative sister taxon, the monobasic Namibian-endemic genus *Mantica* Kolbe, are regarded as an isolated lineage of cicindelines that split off early from the remainder of the tiger beetles (Arndt & Putchkov 1997). The *Manticora* larva shares the characters of drop-shaped abdominal hooks and the absence of the ventral double sclerite between prementum and palpomere I with the larva of *Megacephala* Latreille. The *Megacephala* group also represents an early branch of cicindelines, and a close relationship and possible common origin of these two groups should be examined. A close relationship of *Manticora* and *Megacephala* to basal New-World taxa such as *Pycnochile* Motschulsky, *Omus* Eschscholtz and *Amblycheila* Say is not indicated (Arndt & Putchkov 1997).

REFERENCES

Arndt, E. & A. V. Putchkov, 1997. Phylogenetic investigation of Cicindelidae (Insecta: Coleoptera) using larval morphological characters. – Zoologischer Anzeiger, Jena 235: 231-241.

Bousquet, Y. & H. Goulet, 1984. Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). – Canadian Journal of Zoology 62: 573-588.

Burdick, D. J. & M. S. Wasbauer, 1959. Biology of *Methocha californica* Westwood (Hymenoptera: Tiphiidae). – The Wasmann Journal of Biology 17: 75-88.

Castelnau, F. Laporte, Comte de, 1863. Note sur le genre *Manticora*. – Revue et Magazin de Zoologie (2) 5: 64-73.

Horn, W., 1910. Coleoptera Adephaga, Fam. Carabidae, Subfam. Cicindelinae. – In: Wytsman, P. Genera Insectorum. Fascicule 82A, B, plates 6-15. – Tervuren.

Horn, W., 1915. Coleoptera Adephaga, Fam. Carabidae, Subfam. Cicindelinae. – In: Wytsman, P. Genera Insectorum. Fascicule 82C, plates 16-32. – Tervuren.

Kolbe, H. J., 1885. Die Larve einer *Manticora*. – Berliner Entomologische Zeitschrift 29: 48.

Leffler, S. R., 1980. The larva of *Mantichora* Fabricius. – Cicindela 12: 1-12.

Lucas, H., 1883. (Notes suivantes, 2(). – Bulletin des Séances de la Société Entomologique de France (1883): LXXI-LXXII.

Mareš, J., 1976. New species of *Mantichora* Fabr. (*Coleoptera, Cicindelidae, Mantichorini*). *Mantichora imperator* n. sp. – Journal of Entomological Society of Iran 3: 137-141.

Mareš, J., 1995. Determination key to the males of the genus *Manticora* Fabricius 1792 (Coleoptera, Cicindelidae). – Acta coleopterologia 11: 47-54.

Oberprieler, R. G. & B. Grobbelaar, 1991. Mantichora, the tyrannosaurus of the insect world. – Wilderness Sanctuary 15: 14-16.

Pearson, D. L., 1988. Biology of tiger beetles. – Annual Review of Entomology 33: 123-147.

Péringuey, L., 1893. Descriptive catalogue of the Coleoptera of South Africa. Part 1. Order Coleoptera. Family Cicindelidae. – Transactions of the South African Philosophical Society 7: 1-98.

Poulton, E. B. & G. A. K. Marshall, 1902. Peculiar warning patterns and directive marks in Carabidae and Cicindelidae. Pp. 508-511. – In: Marshall, G.A.K. Five years' observations and experiments (1896-1901) on the bionomics of South African insects, chiefly directed to the

investigation of mimicry and warning colours. – Transactions of the Royal Entomological Society of London (1902): 287-584.

Putchkov, A. V. & E. Arndt, 1994. Preliminary list and key of known tiger beetle larvae (Coleoptera, Cicindelidae) of the world. – Mitteilungen der Schweizerischen Entomologischen Gesellschaft 67: 411-420.

Roer, H., 1984. Zum Vorkommen und Beutefangverhalten des Sandlaufkäfers *Mantichora latipennis* Waterh. (Col.: Cicindelidae) in Südwestafrika/Namibia. – Journal der SWA Wissenschaftlichen Gesellschaft (1982/83-1983/84): 87-93.

Simon, E., 1894. In: Fleutiaux, E., Voyage de M. E. Simon dans l'Afrique australe (janvier – avril 1893). – Annales de la Société Entomologique de France 63: 401-403.

Thiele, H.-U., 1977. Carabid Beetles in Their Environments. A study on habitat selection by adaptations in physiology and behaviour. – Springer-Verlag, Berlin, 369 pp.

Werner, K. & J. Wiesner, 1994. Die Cicindelidae von Namibia (Coleoptera). – Lambillionea 94: 49-80.

Werner, K. & J. Wiesner, 1995. Nachtrag zu 'Die Cicindelidae von Namibia (Coleoptera)'. – Lambillionea 95: 603-610.

Wiesner, J., 1992. Checklist of the tiger beetles of the world (Coleoptera, Cicindelidae). – Verlag Erna Bauer, Keltern, 364pp.