

A journal of world insect systematics

INSECTA MUNDI

0867

How do Vanhorniidae (Hymenoptera) parasitize
Eucnemidae (Coleoptera)?

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Date of issue: May 28, 2021

Center for Systematic Entomology, Inc., Gainesville, FL

Muona J. 2021. How do Vanhorniidae (Hymenoptera) parasitize Eucnemidae (Coleoptera)? *Insecta Mundi* 0867: 1–10.

Published on May 28, 2021 by
Center for Systematic Entomology, Inc.
P.O. Box 141874
Gainesville, FL 32614-1874 USA
<http://centerforsystematicentomology.org/>

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Printed copies (ISSN 0749-6737) annually deposited in libraries

Florida Department of Agriculture and Consumer Services, Gainesville, FL, USA

The Natural History Museum, London, UK

National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

Zoological Institute of Russian Academy of Sciences, Saint-Petersburg, Russia

Electronic copies (Online ISSN 1942-1354) in PDF format

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How do Vanhorniidae (Hymenoptera) parasitize Eucnemidae (Coleoptera)?

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Abstract. The relationship between the beetle family Eucnemidae and the parasitic proctotrupoid family Vanhorniidae is discussed. The only proven host for *Vanhornia eucnemidarum* Crawford in North America is an undetermined species of the genus *Isorhipis* Boisduval and Lacordaire. In Europe, the only known host for *Vanhornia leileri* Hedqvist is *Hylis cariniceps* (Reitter). The biologies of the hosts differ radically and it appears unlikely that they could be parasitized in a typical proctotrupoid fashion in which eggs are placed in or on the host larva. This supports the hypothesis that small Vanhorniidae larvae attach themselves to the newly hatched beetle larvae, before they enter the wood on which they feed. The taxonomy of the genus *Vanhornia* Crawford is briefly discussed.

Key words. False click-beetles, parasites, coevolution, life-history.

ZooBank registration. urn:lsid:zoobank.org:pub:4A0D14B9-FF70-42C2-B499-55DE4A726638

Introduction

The close association between Eucnemidae beetles and Vanhorniidae parasitic wasps remains a dilemma. Although the idea of a highly specialized beetle family having its “own” parasitic wasp family suggests a great evolutionary story, this relationship is still poorly known. Many new records of Vanhorniidae have been published recently (He and Chu 1990, China; Kozlov 1998, Far Eastern Russia; Choi and Lee 2012, South Korea; Doczkal 2017, Germany; Artmann-Graf 2017, Switzerland; Hogan et al. 2019, USA; Belgers et al. 2020, the Netherlands). Further new records are known from Sweden (Forshage i. l.) and Finland (FiBIF).

Most of the new articles discuss the biology of the vanhorniids. These discussions are based mainly on Deyrup (1985) and do not provide new information on the subject. My aim is to introduce the other half of the puzzle into this discussion, the biology of the beetles parasitized.

Two definite host species are known, *Isorhipis* sp. and *Hylis cariniceps* (Reitter). A fair amount is known of the biology of these eucnemids, but that information has not been considered in this context before. In addition, the old host species associations are partly suspect and some of the new records of *Vanhornia* spp. may refer to undescribed wasp species. The overlooked fossil information is pointed out as well.

Materials and Methods

The results presented here are based on a review of the literature and on the author’s personal observations of Eucnemidae, in the wild and in the laboratory. Representative specimens of all observed species were collected and deposited in the author’s personal collection and in the Finnish Museum of Natural History, Helsinki, Finland.

The Biology of *Vanhornia* Species and their Hosts

The original description of *Vanhornia eucnemidarum* Crawford was published in the same journal issue as Van Horn’s detailed discussion of the biology of the Eucnemidae (Van Horn, 1909). Van Horn (1909) included illustrations of the larva, adult beetle and galleries of a eucnemid, *Tharops ruficornis* (Say), later transferred to the genus *Isorhipis* Boisduval and Lacordaire, 1835.

Van Horn (1909) discussed several eucnemid species in his article. He was the first to point out that some species had larvae developing in hard wood, others breeding in soft, rotten wood. He also stated that he had never observed parasites attacking the larvae developing in soft wood. Three species were regarded as hardwood borers: *Isorhipis ruficornis* (Say), *Melasis pectinicornis* Melsheimer and *Nematodes atropos* (Say). However, he did not state which species were parasitized.

Champlain (1922) stated that *Vanhornia* Crawford parasitized *I. ruficornis* without providing any further information on the subject. Brues (1927) based his connection between *V. eucnemidarum* and *I. ruficornis* on finding both species from the windows of a room where substantial amounts of freshly collected wood was stored. As numerous *Isorhipis* specimens were the only eucnemids found, this was a convincing piece of evidence. Finally, Deyrup (1985) demonstrated the association between *Isorhipis* and *Vanhornia* by finding the parasite in the pupal cells built by larvae of *Isorhipis*.

Recent articles discussing *Vanhornia* (Artmann-Graf 2017; Hogan et al. 2019; Belgers et al. 2020) listed *I. ruficornis* as the host species of *V. eucnemidarum*. Hogan et al. (2019) even suggested that the presence of the wasp could be used to map the distribution of the beetle. Hedqvist (1976), when describing *V. leileri*, carefully cited only the original description of *V. eucnemidarum*: “It is a parasite of the larva of the family Eucnemidae”.

Unfortunately, there is a taxonomic problem with all observations mentioning *I. ruficornis*.

Horn (1886) regarded *Isorhipis ruficornis* (Say) and *Isorhipis obliqua* (Say) as synonyms in his revision of North American Eucneminae, at that time regarded as a subfamily of Elateridae. Knull (1946) was the first to realize that Horn had made a mistake and that Say was correct in regarding them as two separate taxa. *Isorhipis obliqua* is by far the more widespread and commoner of the two species (Muona 2000). Van Horn's (1909) illustration shows the strongly keeled pygidium identifying the species he discussed as *I. obliqua*. This led Muona (1993, 2000) to infer that it had actually been the species from which *V. eucnemidarum* was reared. However, this only clarified the identity of the species in Van Horn's (1909) picture; it did not determine the host species of the parasite. Deyrup's (1985) observations are the only ones that prove that the genus *Isorhipis* is a host for *Vanhornia eucnemidarum*. The species identity of the beetle remains ambiguous because of the previous taxonomic confusion in *Isorhipis*. It can be clarified once Deyrup's original specimens are studied – presently they are unavailable because of the COVID epidemic.

Hedqvist (1976) listed *Hylis cariniceps* (Reitter), formerly *Hypocoelus cariniceps*, as the host species of *Vanhornia leileri*, but with no additional information. Leiler (1976), the collector of the type-series of the wasp, provided more information in his review of the biology of the Central European Eucnemidae. The type series of *Vanhornia leileri* was “reared from larvae” of *H. cariniceps* breeding in European spruce (*Picea abies* (L.) H. Karst., Pinaceae). Although further finds of *V. leileri* have been reported from Finland, Germany, Netherlands, Sweden, Switzerland and Far Eastern Russia, no new host observations exist; all of these specimens were collected with traps.

Van Horn (1909) noted that he had never seen parasitization of larvae developing in soft wood. Only *Isorhipis*, *Melasis* and *Nematodes* Dejean larvae, all boring through hard wood, were thus candidates for his observations.

Isorhipis was later proven to be a host for *Vanhornia* (Deyrup 1985). Unfortunately, neither swarming nor egg-laying of the Nearctic *Isorhipis* species has been described. Fortunately, the swarming, mating, egg-laying and larval development have been studied for two Palearctic species, *Isorhipis melasoides* (Laporte) and *Isorhipis marmottani* (Bonvouloir), the latter being very closely related with *I. obliqua* and *I. ruficornis*.

Leiler (1976) provided a detailed description of the mating and egg-laying of *I. melasoides*, breeding in beech (*Fagus sylvatica* L., Fagaceae) in southern Romania. After mating on the surface of a trunk or branch, the females searched for a spot to place the eggs. They inspected suitable surfaces intensively and when a crack, split or an old exit hole of an insect was discovered, they proceeded to lay the very small eggs. Often this took place in a posture like that of many ichneumonids, with the metasoma up high with the help of hind legs and the very long (as long as the length of the beetle) ovipositor directed downward. The ovipositor entered via an opening in the wood, not by drilling through the wood. The beetles preferred to lay eggs one at the time in the exit holes of other beetles, which apparently provide easy access to locations inside the wood. The larvae gnawed their way through the wood straight against the grain forming very narrow galleries tightly packed with frass. Once they were old enough to pupate, they made a chamber close to the surface, usually about 0.5–1 cm deep, in solid wood. Beetles exited through a round tunnel, which was left empty as the frass was pushed out.

The mating and egg-laying behavior of *I. marmottani* is similar to that of *I. melasoides*. The preferred tree in Germany was hornbeam (*Carpinus betulus* L., Betulaceae), a tree with especially hard wood (Muona, pers. obs.). The trees attacked were of modest dimensions, recently dead and at least partly without bark (Fig. 1a). Swarming took place on early afternoon and as the hornbeams formed a bush layer under large oaks at the site, no direct sunlight was present. Beetles ran around the barkless sections of the trunk, males trying to mount females. Immediately after copulation the females started to look for suitable places for egg-laying. Many ovipositing females were observed, all having chosen natural vertical cracks of the trunk (Fig. 1a). Most beetles were covered with fresh white frass suggesting that they were recently emerged (Fig. 1a). The larval galleries were very flat, tightly packed with frass. Pupal chambers were built 0.5–2 cm deep and the beetles exited through round, straight and empty tunnels (Fig. 1b). Leiler (1976) described the egg-laying of *I. marmottani* from Romania, but erroneously reported the species as *Isorhipis nigriceps* (Mannerheim) (Muona 1995). He also followed live beetles in captivity and noted that they were shy of sunlight and easily hid themselves in old galleries of cerambycids and buprestids.

Another widespread hard wood breeding eucnemid clade is the genus *Melasis* Olivier, with many species in the Holarctic and some extending to the subtropics and tropics of the Americas and Asia. The biology of *Melasis* differs from the previously described ones by its highly developed swarming and egg-laying behavior (Palmqvist, 1952). When swarming started, both males and females moved around the trunk of a recently dead solid hardwood and appeared to pay no attention to each other. At some stage females began to bore in the wood and once this had lasted for a while the males suddenly reacted to the females, probably via a chemical cue, and tried to mount them. Females kept boring in wood with a male attached in copula, finally entirely vanishing in the hole. The males remained attached to the females, facing out at the open end of the short burrow, copulation continuing. When the female had completed the construction, she backed out, got rid of the male, turned and backed into the newly made burrow. It is unknown at which point egg laying began. They remained in this position for a few days, seemingly long enough for the eggs to hatch and the minute larvae to enter the wood. If no males were available, females rejected the burrow they made and started to make a new one (Fig. 2a).

This behavior guards the egg-laying site, keeping the eggs and first instar larvae out of reach of parasitoids. Both sexes of *Melasis* are very aggressive against any approaching intruder. At a late stage of swarming, most males have parts of their legs or antennae bitten off.

Melasis buprestoides larvae pupated about a centimeter below wood surface and the beetles exited through a straight tunnel (Fig. 2b). Van Horn (1909) mentions that Burke had collected several *Melasis rufipennis* Horn specimens, which had bored through bark of a dying white fir (*Abies concolor* (Gordon) Lindley ex Hildebrand, Pinaceae) about 2–3 inches deep in solid wood. These were most likely females making burrows for oviposition.

The differences in behavior may explain why *Vanhornia* has not been recorded from *Melasis*, although the development and substrate choice are very similar with those of its close relative, *Isorhipis*, and both genera include widespread, common species over the whole Holarctic.

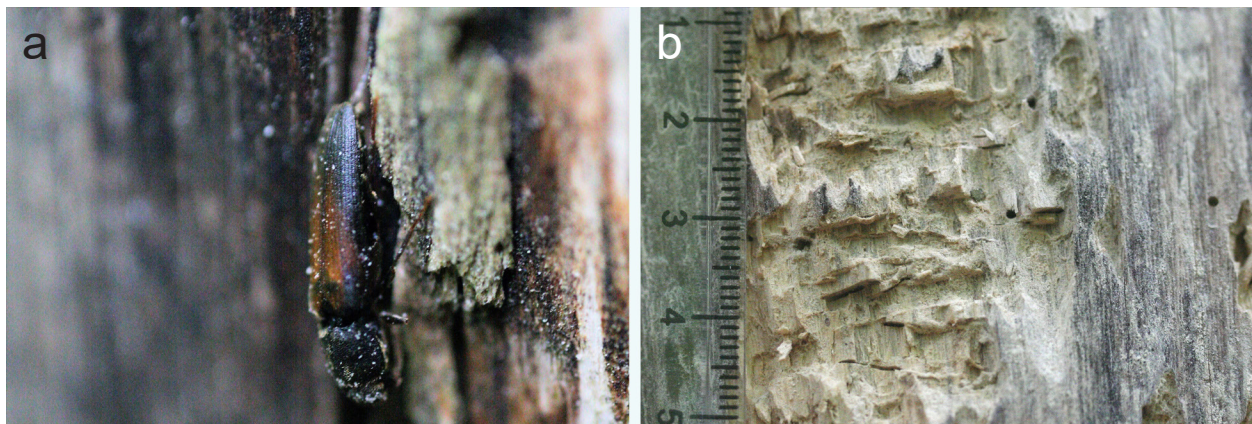


Figure 1. *Isorhipis marmottani* (Bonvouloir) biology. **a**) Female laying eggs in a crack; note the fresh frass on the beetle. **b**) Round, empty exit holes and straight flat larval galleries filled with frass; part of the very hard surface wood removed.

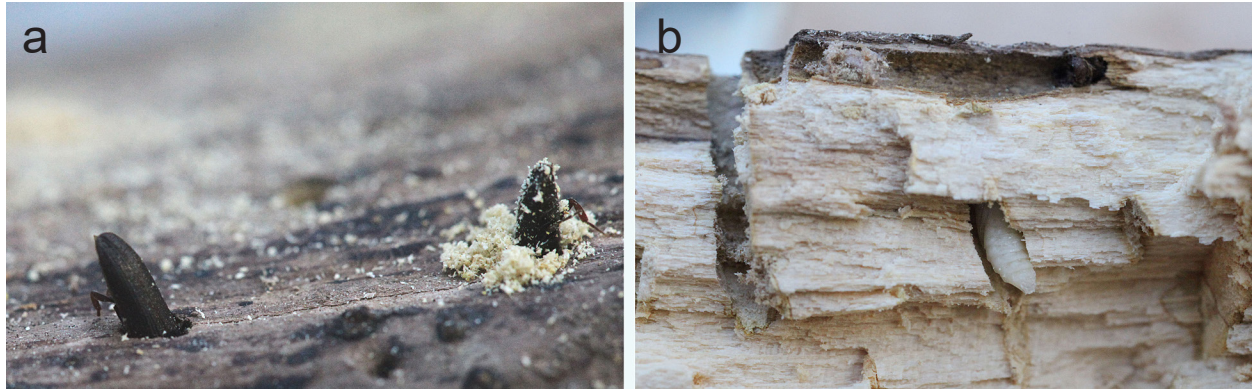


Figure 2. *Melasis buprestoides* (Rossi) biology. **a)** Females making burrows to place their eggs in. **b)** Narrow frass-filled larval galleries end in pupal cells close to surface. After eclosion the beetle bores out leaving a round, empty tunnel. Live pupa in pupal cell in the middle, empty pupal cell and tunnel to surface cut open on the left side.

The biology of another well-studied hard wood borer, *Hylochaes cruentatus* (Mannerheim), followed the same pattern as described for *Isorhipis*, but the ovipositor of this species is much shorter than in *Isorhipis* spp. and the eggs are laid closer to the surface (Muona and Brüstle 2008). *Hylochaes cruentatus* favored laying eggs on walls of old exit tunnels in willows (*Salix* spp.). After a few generations, this created a highly characteristic concentration of exit holes on the surface of the substrate. *Hylochaes cruentatus* eggs were quite large (see Muona and Brüstle 2008) and as they were often laid close to each other, this species might be a good candidate for being parasitized. An interesting observation connected with *H. cruentatus* is the active role of the ovipositor at its apex (Muona, pers. obs.). When searching for an egg-laying location, beetles walked slowly along surfaces of freshly broken dead willows. The fairly short ovipositor moved rapidly and continually touched the surface with its apex (Fig. 3a). It appeared clear that the beetle actually “sniffed” with its ovipositor in order to find a good fungus-rich location.

Van Horn (1909) listed *Nematodes atropos* (Say) as a hard wood borer as well. The biology of *Nematodes* species is not completely understood, but it differs from that of *Isorhipis* and *Melasis* substantially in the development of larvae (Otto 2017, Muona and Teräväinen, 2020). Otto (2017) observed females ovipositing on wood surfaces in a laboratory situation. The newly hatched larvae were free-living triungulins actively searching for suitable openings in the wood. This extraordinarily interesting behavior may have been caused by the laboratory conditions, as no other eucnemid beetle is known to do this in nature and this one instance in a controlled setting

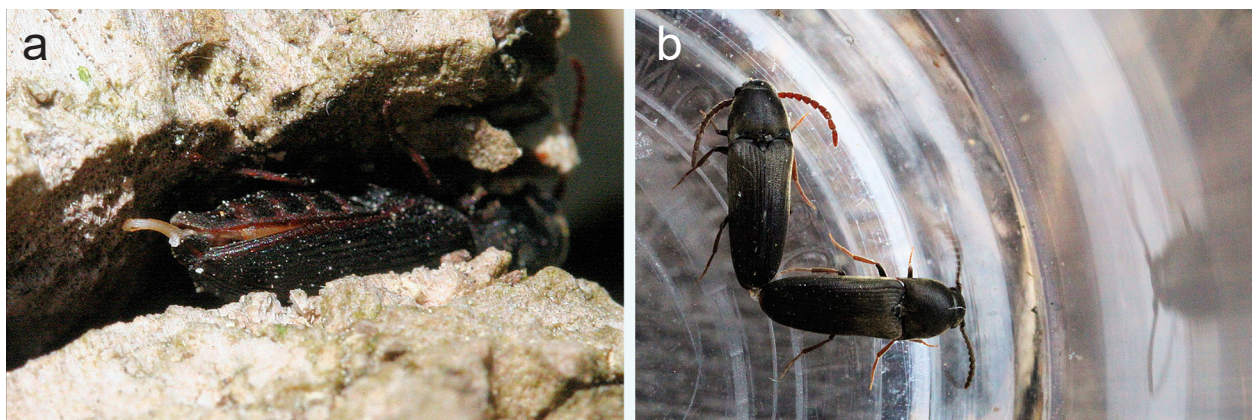


Figure 3. Eucnemid behavior. **a)** *Hylochaes cruentatus* (Gyllenhal) searching for good location to lay eggs in a crack on Jolster (*Salix pentandra*). Note the ovipositor used for finding the right spot. **b)** *Hylis procerulus* (Mannerheim) mating in a vial, male on left, female on right. Note the quivering left antenna of the female, a typical feature for eucnemids.

may not be representative. All *Nematodes* species studied by the present author have very long ovipositors, 1.5–2 times as long as the female body length. This suggests that eggs can be laid very deep in the wood and it would be surprising if they were normally used in laying eggs on the surface of the wood.

The hard wood boring eucnemids with strong mandibles form a small minority in the family; many of the extant eucnemid species have larvae with minute mandibles, a chisel-shaped head with lateral serrations and use internal liquid pressure to move through soft wood infected by fungi (Lucht 1981; Muona and Teräväinen 2008, 2020 and references there). The host of *V. leileri*, *Hylis cariniceps*, belongs to this group. The larval development of the *Hylis* species is reasonably well known, although partly not published (Leiler 1976, Lucht 1981, Muona, pers. obs.).

The Palearctic *Hylis procerulus* (Mannerheim) is the best-studied *Hylis* species (Muona, pers. obs., Finland). It bred in brown-rot European aspen (*Populus tremula* L., Salicaceae). When swarming started, the beetles moved with great speed along logs. The details of what happened during this time could be appreciated only by catching the beetles and filming a pair in a controlled environment, a closed, round dish. In such an experiment the male kept running along the edge of the dish and paid no attention to the immobile female. After a while the female opened her elytra slightly and shivered the tip of the abdomen. This caused the male behavior to change. He stopped and started to approach the female in a zig-zag pattern indicating that he followed the strongest chemical concentration of a pheromone. After finding her he placed himself behind her with mouthparts close to the abdominal tip. Then he started to palpate the female and after a moment she took off with great speed, the male following as if glued to her, continuously palpating her abdominal tip. All this took place while the beetles ran with great speed, like a miniature train. The actual copulation could not be observed in nature, as the beetles always hid under loose bark. However, when they were placed in a dish one could see the female finally stop and open the elytra slightly more. Then the male came to her side, tips of abdomens close to each other, aedeagus projecting in a nearly straight angle to side. The act took place in this unusual position, side by side (Fig. 3b). This appeared to be an adaptation to mating in safety under bark, a feature not reported for other eucnemids earlier.

In addition to aspen, *H. procerulus* breeds in spruce (*Picea abies*) as well. The eggs were laid in cracks or other openings, frequently on the underside of fallen logs. The ovipositor is fairly short and delicate and the eggs cannot be placed very deeply. The wood has to be fairly moist and heavily infested with brown-rot fungus. The substrate structure is such that the wood can be broken into pieces by hand. The larvae move around without leaving actual tunnels, but their advance can be traced by following slightly displaced wood fibers and the larval skins, which are shed off along the path and easily detected because of the strongly sclerotized dark head capsule. The pupal chambers are dug very close to the surface, mostly less than 1 cm from the surface.

Microrhagus Dejean is another genus associated with *Vanhornia*, albeit only by collection from the same site. Belgers et al. (2020) mentioned that one *Microrhagus lepidus* (Rosenhauer) had been caught two weeks earlier at the site where *V. leileri* was taken, both apparently attracted by light.

Suitable large logs of European aspen (*Populus tremula*) can be used by *H. procerulus*, *Microrhagus pygmaeus* (Fabricius) and *M. lepidus*. *Hylis* larvae keep to the brown-rot regions and *Microrhagus* larvae develop in the white-rot areas. Large numbers of all these species have been observed to develop in the same logs in Finland over a period longer than a decade (Muona, pers. obs.). The biology of all these species is quite similar, with the exception of the fungus type required by the larvae. The other difference is in swarming, with *Microrhagus* males climbing on the females without any prior special behavior. This swarming behavior includes frequent attempts to penetrate both males and females, as well as cutting off the antennae or legs of any putative partner. Since eucnemids are known to primarily use their complex antennae and antennal receptor systems for communication, the swarming is likely triggered by strong chemical stimuli.

How Do the Vanhorniidae Attack Their Hosts?

The two hosts unambiguously associated with *Vanhornia*, *Isorhipis* and *Hylis*, develop in very different types of wood. An obvious question is if the differences in the biology of the hosts correspond to the method of how *Vanhornia* attacks the beetles.

As shown by Quicke et al. (1994), *Vanhornia* has a unique ovipositor with several unusual features. The dorsal valve forms a solid supporting rod-like structure that is connected to the interlocking mechanism by

membranous walls only, the ventral valves being overlapping and not unlike those of Proctotrupidae. One would expect the large sheaths to play a supporting role for the ovipositor, but as Deyrup (1985) described, it is unclear whether the sheaths actually penetrate the substrate at all. The whole structure is flexible and the ovipositor can be extended from between the sheaths, at least to some extent (Deyrup 1985). Nothing suggests that the *Vanhornia* ovipositor can penetrate solid wood and it clearly is not a drill. However, this kind of an ovipositor could reach the eggs of hard wood borers, which are placed deep in the tree. *Isorhipis* has a similarly long and flexible ovipositor for placing the egg in cracks or holes already present in the wood. By either following the beetle or being able to detect its actions chemically, *Vanhornia* would be able to find the host egg (see Deyrup 1985). Once the *Isorhipis* larva enters the solid wood, its characteristic tunnel can be reached only with an ovipositor capable of drilling, something *Vanhornia* does not have. Reaching the host would require the wasp larva to wait for the beetle larva to hatch and attach to it at this stage.

Another possibility could be targeting the pupal chamber. The fully developed *Isorhipis* larvae build their pupal chambers close to the surface, so laying the eggs in the mature beetle larva or pupa is a possibility. However, this requires a method of penetrating solid wood in the case of *Isorhipis*. Van Horn (1909) mentioned that eucnemids generally extend the larval tunnel “within a hair’s breadth of the surface” past the pupal chamber before pupating, in order to facilitate the beetle’s exit. The present author has not observed this in *Hylochaeres*, *Isorhipis* or *Melasis*. They all have powerful mandibles for creating the tunnel needed to exit from the wood.

Deyrup (1985) found the *Isorhipis* larval skin in the parasitized pupal chamber, but no remains of a pupa. The pupal chambers of eucnemids often appear to contain only the larval skin besides some frass, so the apparent absence of the pupal remains may not mean much.

How the *Hylis* larvae are parasitized is unclear. The softer substrate might be penetrable via support provided by the ovipositor’s dorsal valve design. This could be easiest when the beetle larva starts building the pupal chamber close to the surface of the log softened by the brown rot. This type of wood, with strong fungal infestation, tends to have a matrix-like structure and may provide easy entry. Attacking the fully developed larva or pupa in the pupal chamber close to the outer surface is also possible.

If it turns out that *Microrhagus* is a host as well, *Vanhornia* most likely parasitizes it the same way it parasitizes *Hylis*. Townes and Townes (1981) reported that “Babiy had observed *V. eucnemidarum* females crawl along barkless hardwood logs”, occasionally pause over a crack, unhinge the ovipositor into the crack and pass the ovipositor along the crack. This is similar to the oviposition of *Isorhipis*, suggesting that the wasp targets the beetle eggs deep in the cracks rather than searches for larvae or pupae in the pupal cells close under the surface in hard wood.

Proctotrupoids usually lay eggs in or on host larvae (Masner i. l.). Larvae of *Hylis* species might be accessible to *Vanhornia*, but it is very hard to see how *Isorhipis* could be parasitized this way. A more feasible scenario is that *Vanhornia* seeks freshly laid eucnemid eggs and lays its own eggs by them. The wasp larvae hatch sooner than the eucnemid larvae and attach themselves to the beetles once these are ready to enter the wood. This method would be equally useful for parasitizing both *Isorhipis* and *Hylis*, but it would not work for utilizing *Melasis*. On the basis of the Eucnemidae species parasitized and the structure of the Vahnornidae ovipositor it appears likely that the solution Deyrup (1985) suggested is the right one. Vahnornids search for freshly laid eucnemid eggs and place their own eggs by them. The wasp larva hatches first and then stalks the beetle larva, which enters the wood carrying its own death with it.

The Mandibles

All adult Eucnemidae have strong and prominent endodont mandibles (Muona 1993). Muona and Teräväinen (2020) showed that although nearly all extant eucnemid larvae have exodont mandibles, the variation is considerable and there is an evolutionary sequence starting from toothless endodont mandibles, to endodont mandibles with lateral teeth and ending in a true exodont condition with lateral teeth, and finally to entirely miniature and immobile spike-like mandibles.

In practice, exodont mandibles are a tool for separating instead of crushing. *Isorhipis* larvae have powerful exodont mandibles and *Hylis* larvae have immobile, tiny exodont mandibles (Muona and Teräväinen 2020).

These two species use their adult mandibles the same way and their larval mandibles in a different way. Both adult beetles need endodont mandibles to bore their way out from the wood. *Isorhipis* larva needs exodont mandibles for gnawing the galleries inside the hard wood whereas *Hylis* larvae have miniature exodont mandibles of now practical use, moving inside soft wood with liquid pressure and chisel-shaped head capsule with lateral teeth (Muona and Teräväinen 2008).

Vanhorniid wasps have well-developed exodont mandibles. Besides Alysiini braconids, this particular feature is very rare in Hymenoptera. Wharton (1984) described how exodont Alysiini mandibles were used for escaping from the host puparium and provided evidence that they are also used for penetrating soil in search of fly larvae. The eucnemid pupae are soft and parasitoids can easily leave them through the pupal skin. However, getting from pupal chamber to the exterior of the wood substrate is another matter. It might be fairly easy in the case of *Hylis*, but with respect to *Isorhipis* it is hard work, even if for a short distance. It is clear that adult *Vanhornia* must be able to do it, however “unsuitable” the mandibles are, as the beetles in question do not prepare a nearly complete escape tunnel before pupating deeper in the wood.

Muona (1993) showed that the lignicolous eucnemids evolved from soil-dwelling forms (see also Muona and Teräväinen 2020). The Vanhorniidae – Eucnemidae relationship may well have originated at the same time period, the Jurassic, as primitive proctotrupoidea are certainly old enough for that. If this is the case, Wharton’s observations (1984) with respect to Alysiini are relevant. Vanhorniids may have searched for soil dwelling eucnemids as Alysiini search for fly larvae. Later on, when the soil-dwelling eucnemids became rarer and the lignicolous eucnemids dominant, vanhorniids switched to these. In such a scenario the exodont wasp mandibles may be pleiomorphies that do not represent adaptation specifically related to wood feeding beetles.

Some General Considerations

Sharkey et al. (2012) provided the modern hypothesis for Proctotrupoidea evolution, based on all extant taxa and a thorough analytical approach. On the basis of their total support tree, Vanhorniidae are the sister-group to the clade (Heloridae + Proctotrupoidea). This dates Vanhorniidae firmly in the Jurassic as many Heloridae fossils are known from that period. Chang et al. (2016) described the Cretaceous eucnemid *Palaeoxenus sinensis* Chang, Muona and Teräväinen, and Li et al. (2021) described another Cretaceous eucnemid, *Rheanischia brevicornis* Li, Chang and Muona, showing that lignicolous eucnemids belonging to different clades already existed 125 Mya. Though the host-parasite interaction of the wasps and the beetles has not yet been confirmed in the fossil record, the presence of both taxa in the Cretaceous strongly suggests that their relationship is ancient indeed.

Serrano et al. (2019) published the first study documenting chemical communication in eucnemids. They showed the presence of several male-produced compounds, a blend of two of them attracting both sexes of *P. dohrnii*. Observations of *Isorhipis*, *Melasis*, *Hylis* and *Microrhagus* swarming all suggest chemical cues and Muona (1991, 1993) has shown that Eucnemidae have several different types of receptors in different combinations on antennomeres. Chemical communication is advantageous for insects with long solitary development in wood and short mating and egg-laying activity period, but it also opens a path for a parasitoid to find the host. Both *Isorhipis* and *Hylis* species tend to breed in the same logs for a long time, a feature shared by many eucnemids. Such colonies are excellent breeding sites for the parasitoids, but they will eventually be required to locate new sites. Because the beetles use fungus infesting the wood as their main food source, an obvious choice for the parasitoid to use as the long-distance cue would be the fungus. Also, if Deyrup’s (1985) hypothesis is correct, the wasps would need to be able to locate the sites where the beetle laid eggs. Considering what is known about parasitic wasps (e.g. Quicke 2015) there are many possibilities for that, starting from learned behavior, beetle “footprints” and chemicals associated with the beetle skin or the laid eggs. As eucnemids do not attack healthy trees, the compounds emitted by trees with mechanical damage are another possible long-distance cue for both the beetle and the parasitoid as eucnemids are known to fly to freshly cut timber in the tropics (J. Sedlacek, pers. comm.)

Taxa

Vanhornia eucnemidarum Crawford (type locality USA, Maryland, Montgomery Co., Silver Spring), the type species of the genus *Vanhornia*, was reported recently from some twenty-five Central and Eastern US states, Oregon and three Canadian provinces (Hogan et al. 2019). In addition to Nearctic locations, it has been reported from South Korea (Choi and Lee 2012) and Germany (Belgers et al. 2020). Both the Korean and German records of *V. eucnemidarum* should be re-evaluated. On the basis of the description, the Korean specimen does not appear to be *V. eucnemidarum* (Choi and Lee 2012). Even if possible wear is taken into account, the spacing, shape and size of the mandibular teeth appear different in the two species. The carinae of the propodeum seem to differ as well. According to Timokhov and Belokobylskij (2020) this record may be based on their new species, *Vanhornia yurii* Timokhov and Belokobylskij. The German records, if correct, suggest an introduction.

The second included species, *Vanhornia leileri* Hedqvist (type locality Sweden, Södermanland, Tullgarn) has been listed from five locations in Sweden (Forshage i.l.), Far East Russia (Kozlov 1998) and Switzerland (Artmann-Graf 2017). Finland (FinBIF 2021) and Netherlands (Belgers et al. 2020) are the most recent additions to this list. Considering the extensive distribution, these specimens should be compared to verify the situation.

The third Vahnorniidae species, *Vanhornia quizhouensis* (He and Chu 1990) (type locality China, Guizhou Province, Huishui County; described as *Sinicivanhornia*) is known from two locations in China (Artmann-Graf 2017). He and Chu (1990) based their new genus *Sinicovanhornia* on three features: (1) slightly different position of antennal sockets, (2) four mandibular teeth and (3) ovipositor sheath distinctly longer than abdomen. *Vanhornia leileri* has four major mandibular teeth as well. This is shown in image 2B in the original description, although in the text the number of teeth is by mistake reported as “5” (Hedqvist 1976). There does not seem to be any difference in the ovipositor between the three taxa on the basis of the original descriptions as well as later images (e.g., Deyrup 1985). This leaves the slight difference in antennal socket placement as the sole distinguishing generic character. This is hardly a reason for erecting a genus. There are no evolutionary novelties demonstrating sister-group relationships between the two genera, just slight differences between species. Kozlov’s (1998) synonymy of these genera is clearly justified.

According to Artmann-Graf (2017), Masner knew of two possibly undescribed species, one from Japan and one from the Western USA, Oregon (see Townes and Townes 1981). The latter one, if separate from *V. eucnemidarum*, very likely refers to the species Hogan and al. (2019) reported as proof for the continent-wide distribution of *V. eucnemidarum*. Masner (i. l.) confirmed the possibility of a second species in the Western North America, but pointed out that the matter remained unclear.

Other Parasitic Wasps Connected with Eucnemidae

Vahnorniids are not the only parasitic wasps reported to attack eucnemids. Leiler (1976) lists three other cases, with the wasps identified by Hedqvist and Käärrik.

Dibrachys fuscicornis (Walker) (Pteromalidae) [as “*fircicornis*”] was reared from a larva of *Eucnemis capucinus* Ahrens. This species is known to parasitize Tenthredinidae wasps, but other *Dibrachys* are known to parasitize an extensive list of species, although not Coleoptera. They are known to be both parasitoids and hyperparasitoids (Doganlar 1987).

Calosota acron (Walker) (Eupelmidae) was found in the pupal chamber of *Melasis buprestoides* (Rossi). This species is a hyperparasitoid, so the real host remains unknown (Gibson 2010).

Sclerodermus “n. sp.” (Bethylidae) was reared from the same wood pieces as *Isorhipis marmottani* (Bonvouloir) (incorrectly originally published as *I. nigriceps*, see Muona 1995). Considering the biology of *Sclerodermus harmandi* (Buysson) (Hu et al. 2012), it is difficult to see how the wasp could have reached the *I. marmottani* larvae. A more likely host might be the anobiid *Oligomerus brunneus* (Olivier), reared from the same piece of wood as the eucnemid.

Acknowledgments

I am grateful for the help and advice many colleagues gave me: M. Deyrup (USA), M. Forshage (Sweden), L. Masner (Canada), M. Sörensson (Sweden) and L. Vilhelmsen (Denmark). I also thank J. Carpenter and R. Otto for their reviews of the manuscript.

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Received January 14, 2021; accepted April 23, 2021.

Review editor Elijah Talamas.