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BIOLOGICAL OBSERVATIONS ON THE GENUS *CERAMIOPSIS* ZAVATTARI (INSECTA: HYMENOPTERA: VESPIDAE: MASARINAE)

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Abstract.- Details of the biology of the wasps of the genus *Ceramiopsis* are described, mainly covering flower visiting behaviour, nest architecture and minor details on other ethological traits.

Resumen.- Se describen detalles de la biología de las avispas del género *Ceramiopsis*, cubriendo principalmente comportamiento en la visita de flores, arquitectura de nidos y detalles menores sobre otras características etológicas.

About a decade ago Garcete-Barrett & Carpenter (2000) gave a key and complete descriptions in order to recognize the two species of pollen wasps of the genus *Ceramiopsis* Zavattari, hitherto considered a single species: *Ceramiopsis gestroi* Zavattari and *Ceramiopsis paraguayensis* Bertoni. In the same work they recorded the flower species visited by each species. The only biological data before this publication were given by Bertoni (1918) in his description of *Ceramiopsis paraguayensis*, where he just mentioned a subterranean nest with an entrance turret that he interpreted as an anthophorine nest that the wasp was probably cleptoparasitizing. The internal structure of the nest was not described and his interpretation of lifestyle was innacurate, as cleptoparasitic habits have been never observed in masarine wasps.

The behaviour of adult masarines in flower visiting, water gathering and nesting has potentially interesting evolutionary implications and have been surveyed for several South African and some Palaearctic, Nearctic and Australian species (summarized in Gess 1996; Gess et al. 1997; Mauss et al. 2006; Mauss 2006, 2007; Neff & Hook 2007). Publications on these aspects of life have been scanty for neotropical species (Claude-Joseph 1930; Zucchi et al 1976; Neff & Simpson 1985; Mechi 1999a, 1999b).

This work summarizes details on the behaviour and life habits (flower visiting, water gathering, territoriality, mating behaviour and nesting) of species in the genus *Ceramiopsis*, based on intensive field observations.

MATERIAL AND METHODS

This paper is the result of a series of field observations made from January to May of 1997. Altogether ten fieldtrips were undertaken to five localities near Asunción (Paraguay): Pirayú (25°28’49.58"S 57°13’17.39"W), Puente Remanso (two sites: 25°10’57.81"S 57°32’19.74"W and 25°11’20.56"S 57°32’48.58"W), Villa Hayes (25°05’43.29"S 57°30’51.53"W) and Río Confuso (25°06’20.73"S 57°32’48.02"W). Some casual observations were also made along the following years in other places: Puerto Tres Palmas (21°44’41.31"S 57°56’59.83"W), San Carlos del Apa (22°14'02.37’’S 57°17’48.88’’W), Estancia Maria Auxiliadora (22°45’36.32’’S 57°26’15.14’’W), Estancia San Luis (22°26’30.06"S 57°30’39.43"W) Puerto Casado (22°17'22.40"S 57°56'48.60"W) and Remansito (25°08’44.70’’S 57°33’21.60’’W). The sites had in common the presence of a water body supporting populations of the plants visited by the insects, the habitats varying from transitory puddles and ponds (Fig. 1A) or creek banks with rooted aquatic or semiaquatic vegetation, to rafts of floating vegetation along the banks of the Paraguay River (Fig. 1B). The

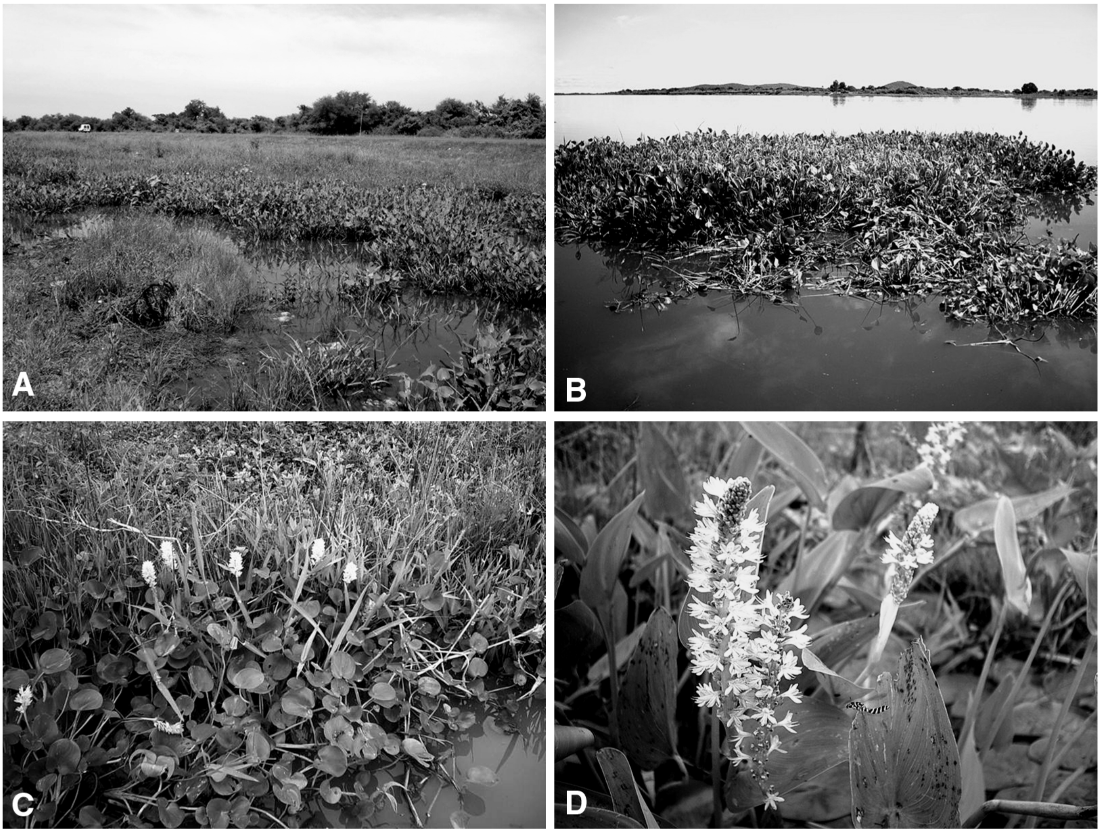

Fig. 1. Habitats and views of the plants visited by *Ceramiopsis* wasps. A) puddle with patches of *Pontederia cordata* at Remansito [photograph by Marcel G. Hermes]. B) Raft of *Eichornia crassipes* and *Eichornia azurea* floating on the Paraguay River at Puerto Casado. C) Patch of *Pontederia rotundifolia* along a puddle at Puerto Casado. D) Inflorescences of *Pontederia cordata* at Puerto Casado, with a female of *Ceramiopsis gestroi* in stationary flight near the closest inflorescence.

ethogram and behavioural details were taken from direct observations made by both authors and video shooting made by the junior author using an 8 mm Sony Handycam CCD-TR51. We were able to collect two nests of *C. paraguayensis* by taking out the whole earth mass containing each nest, marking the main shaft with bright colored paint and carefully disecting the earth mass with the aid of needles. The general function of the mouthparts was investigated by study of the videos taken, by direct observation of individuals kept alive in a glass tube closed with wire mesh on one side and cork on the other side, and by dissection of some individuals by the senior author. The position of various structures of the flowers for comparison with the position of the mouthparts of the wasps during flower visitis was traced from flower specimens fixed in a mixture of ethanol, water and formaline (ratio: 15:15:70). Voucher specimens of the wasps were collected and are cited in the revision (Garcete-Barrett & Carpenter 2000).

BIOLOGY AND BEHAVIOUR

DAILY ACTIVITY: We certainly do not have a complete and separate record of daily activity for each species. From field notes made in March of 1997 we can extract that the activities of *C. paraguayensis* apparently started at about 09:00 hs and those of *C. gestroi* ended around 16:00 hs. The daily activity of adult *Ceramiopsis* wasps seems to be limited to the peak hours of insolation.

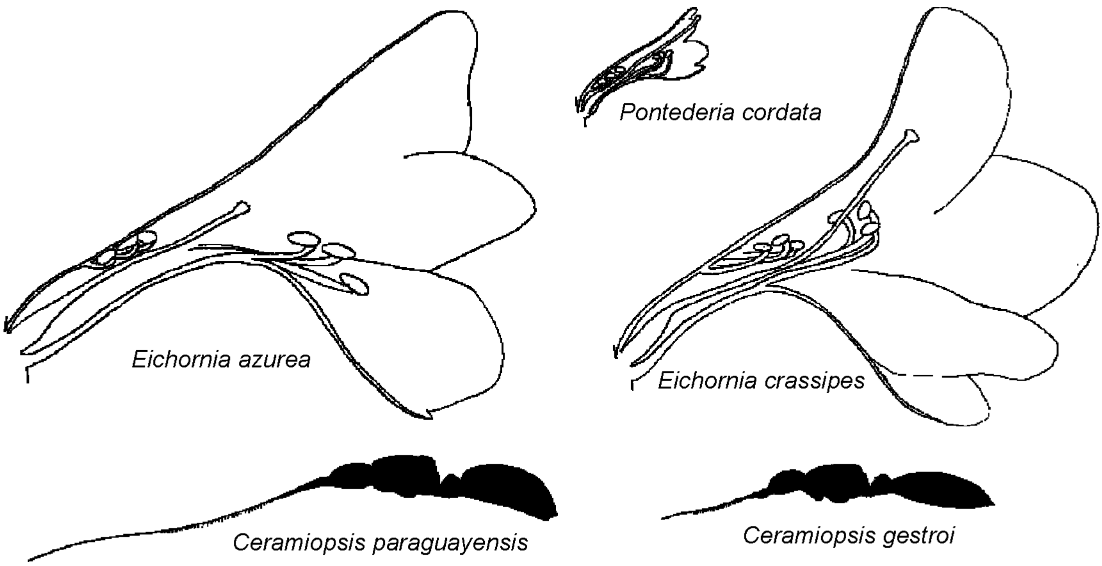

Fig. 2. Profiles of both *Ceramiopsis* species and of some of the flowers visited by them to demonstrate wasp/flower fit. All the dawings are made at the same scale in order to compare proboscis lenght with the depth of the corolla tubes.

Flower visiting and interspecific competition: From the evidence we have up to now, *Ceramiopsis* wasps are restricted to visit flowers of the aquatic plant family Pontederiaceae, with the genera *Eichornia* and *Pontederia* being recorded so far.

Owing to the different size of their mouthparts (Fig. 2), both wasp species seem to be restricted by the size of the individual flowers and normaly have a preference for one of the aforementioned genera of Pontederiaceae. The body size of the wasps is just slighly different, but *Ceramiopsis gestroi* has a shorter proboscis and prefers the small flowers (Figs 1C and 1D) of *Pontederia* (*P. cordata* L. and *P. rotundifolia* L. f. —new record from Alto Paraguay: Puerto Casado, in November of 2006—), while *C. paraguayensis* has a remarkably longer one and seems to be restricted to the large flowers of *Eichornia* (*E. azurea* (Sw.) Kunth and *E. crassipes* (Mart.) Solms) (Garcete y Carpenter 2000).

Beyond this, our observations seem to verify an obligatory behavioural preference of each wasp species for a particular genus of flowering plant. There is a couple of exceptions that probably do not break the rule. One was the case of a male of *Ceramiopsis paraguayensis* briefly patroling an inflorescence of *Pontederia cordata* —males do not collect pollen, and that was just probably part of territorial displays—. The other case, described in the following paragraph, looked like failed attempts or an oportunistic situation showing some lack of behavioral skills:

At Pirayú, on warm days (at least around 25°C), when the populations of both wasps were active, each wasp species normally visited on ly flowers of the preferred genus, even though patches of Eichornia azurea and Pontederia cordata were just separated by a few meters. During the cloudy morning of April 9th of 1997, with a temperature of 22°C, the situation was different. Individuals of *C. paraguayensis* were inactive and did not visitin any flowers. They were resting on the leaves of the vegetation along the creek instead, and just occasionally performed short flights to land on nearby leaves. At the same time, individuals of *C. gestroi* were fully active, and visited not only flowers of *P. cordata*, but also those of *E. azurea*. While the performance during the visits on *P. cordata* was as quick and fluid

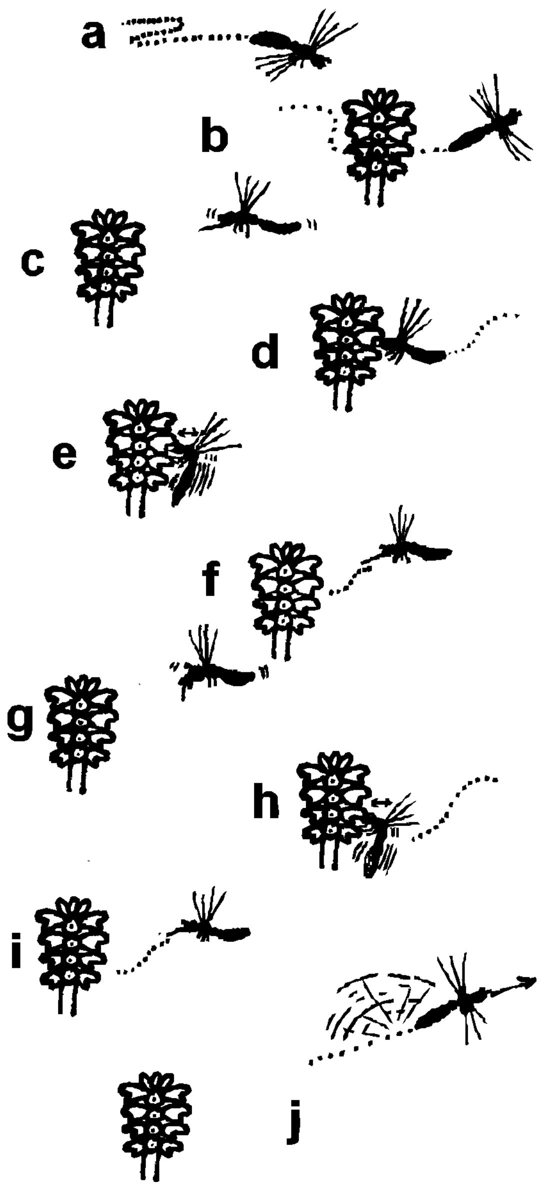

Fig. 3. Generalized ethogram of *Ceramiopsis gestroi* visiting flowers of *Pontederia cordata*. The letters represent the events described in the main text.

as observed and filmed on previous occasions, the visiting performance during visits to flowers of *E. azurea* looked clumsy and slower, without a direct entrance to a selected flower but with a repeated back and forth landing attempt. Some of these attempts ended with the wasp desisting of entering to the flower and leaving it. These observations seem to indicate that *C. gestroi* can visit flowers of *E. azurea* in an opportunistic way when *C. paraguayensis* is absent or inactive.

FLOWER VISITING BEHAVIOUR: The behaviour pattern reconstructed in the ethogram (Fig. 3) is mainly based on the pattern and sequence followed by females of *C. gestroi* when visiting *P. cordata*, as the small size of the flowers allowed a more complete observation. Some details about each event and the variation observed in males and in *C. paraguayensis* or while visiting the larger flowers of *Eichornia* are commented upon in separate paragraphs. The standardized sequence of events is as follows:

a) Overall patrolling of the patch of vegetation; ***b***) approaching and flying around a particular inflorescence; ***c***) short stationary flight in front of the inflorescence during which the proboscis is explosively extruded; ***d***) fast entrance to a particular flower directly from the front; ***e***) repeated shaking of the body back and forth; ***f***) backward flight to leave the flower; ***g***) stationary flight in front of the flower during which the proboscis is quickly pulled down a couple of times with the fore legs; ***h***) repetition of events *d-g*; ***i***) last repeating of event *f*; ***j***) redirection of the body in flight while the proboscis is retacted inside the oral cavity and subsequent leaving of the area in normal frontal flight.

During the events ***c***, ***d*** and ***g*** the metasoma is kept in a crescent-shaped form (see also Fig. 1D), with the venter arched downward and the tip raised up. This position is particularly conspicuous in *C. gestroi*. Once the proboscis is extended during event ***c***, it is kept out for the duration of the complete behavioural sequence performed at a particular inflorescence and is not retracted untill the wasp finally leaves the inflorescence, during event ***j***. Event ***e*** is most evident in *C. gestroi* when visiting *P.cordata*, as the metasoma hangs down, acting as a counterweight while performing a series of four to six violent shakes.

The metasoma is unable to hang down and the shakes are very limited in energy when either wasp species visit flowers of *Eichornia*. We cannot be assured if the cleaning of the glossa is obligatory during event ***g***. Some video shots seem to show sudden disappearance and reappearance of the glossa and in a particularly close one a female of *C. gestroi* rapidly pulls and releases her glossa down under the body with both fore legs.

In males event ***a*** is the predominant one and could be related to territorial behaviour or couple searching, and the complete visit sequence is faster than in females. Males have reduced ventral glossal processes and the dissections of males showed an almost empty diggestive tract, so flower visiting could be made just as part of the territorial performance, and at most for nectar and just a few pollen uptake. We have not seen separate behaviours for nectar and pollen retrieval as confirmed *e. g.* for the South African species *Jugurtia codoni* (Gess et al. 1997) and we judge that nectar and pollen uptake are performed simultaneously by means of the long glossa that bears a row of ventral processes on each of its elongate lobes.

TERRITORY AND SEXUAL BEHAVIOR: As explained above, males spend most of the time patrolling along the flowering patches and, when they choose an inflorescence to fly around, they visit the flowers very briefly or even not at all. Therefore, males probably take up only little amounts of food while looking for females or defending a chosen territory. At Pirayú, a male of *C. gestroi* was observed to repeat the same flying path over a patch of *P. cordata* again and again. On several ocasions at different places we have seen males of *C. paraguayensis* flying around a particular *Eichornia* inflorescence and chasing other approaching males, though not very insistently and soon becoming tolerant.

We did not perceive complete copulations, but we observed two probable copulatory attempts in which the male approached the female and tried to get on her back violently. However, in both cases this was unsuccessful as the female finally released herself: the first case was a couple of *C. gestroi* in a flower of *P. cordata* and the second one a couple of *C. paraguayensis* kept alive in a glass tube.

WATER COLLECTING: Under natural conditions, *Ceramiopsis paraguayensis* seems to be able to alight on the water surface as reported for some South African species of *Ceramius* (Gess 1996, plate 9). The only free observation was that of a female collected in Villa Hayes while landed on the water surface covered by diminutive floating aquatic ferns of the Genus *Azolla* and taking up water directly from the surface without extension of the proboscis.

Nevertheless, under different conditions the wasps use the proboscis for water uptake. Several males and females of *C. paraguayensis* were kept together in a glass tube and used the glossa to take either the condensation on the glass walls or water drops given to them. This occasion gave the opportunity to observe that the glossa was extended explosively and then retracted back gradually into the oral cavity by the action of the maxillae, that grabed the glossal lobes as if they were hands pulling back a couple of ropes.

Water collected in the crop is normally used by vespids in nest making, either as softening agent for burrowing in hard soil or as bonding agent for self made mud used in cell building (West-Eberhard et al. 1995; Gess 1996; Gess et al. 1997). In contrast, some apoid wasps (e. g. in the genera *Sceliphron* an *Trypoxylon*; Hanson & Menke 1995) take mud instead of water directly from the waterfront. Judged from the nest architecture of *C. paraguayensis*, both vespid uses of water for nest building seem to occur in *Ceramiopsis*.

GROOMING AND FOOD TRANSPORT: Most members of the genera *Pontederia* and

Eichornia have deep and narrow corolla tubes and are tristylous, which means that the anthers and stigmas are placed at three different depth levels in relation to the length of the tube and, moreover, the pollination only takes effect when pollen of a certain anther level is transferred to the stigma of the same level (Alves-dos-Santos 1999). Several oligolectic bee species that are specialized in pollen from the flowers these genera of *Pontederiaceae* have developed specialized hairs on their mouthparts in order to take up pollen from the shorter (deeper) anthers of these flowers (Alves-dos-Santos 1999, 2003).

The greatly elongate glossal lobes of *Ceramiopsis* wasps bear a line of ventral processes (Richards 1962; Garcete & Carpenter 2000). When the proboscis is completely introduced into the corolla tube, these ventral processes fit in position with the short anthers of the flowers (Fig. 2). The fast frontal entrance to the flower with extended proboscis during event ***d*** and the back and forth shaking performed during event ***e*** are quite similar to the behaviours described by Alves-dos-Santos (2003) for species of *Ancyloscelis*, *Florilegus* and *Paratetrapedia* that are also specialized in pollen uptake from flowers of *Pontederia* and *Eichornia*. It seems evident that the ventral glossal processses of *Ceramiopsis* have the same function as the hair brushes on the mouth parts of these bees.

In contrast to most bees, that transport pollen in external structures of the exoskeleton, masarines carry pollen in the crop (Gess 1996). Neff & Simpson (1985) suggested that the distorted and hook-setose fore tarsi of female *Trimeria rhachiphora* (Schletterer) [cited as *T. buyssoni* (Brèthes)] play an important role in pollen uptake. Indirect pollen uptake from the exoskeleton with fore tarsal pollen brushes has also been observed in pollen wasp species of the genus *Ceramius* (Mauss 1996, Mauss et al. 2006) and *Celonites* (Schremmer 1959, 1961, Mauss 2006). The videos of *C. gestroi*, during flower visiting and grooming seem to verify a transport function of the foretarsi. We assume that the proboscis is brushed all along with the tarsal hairs while being pulled down and back during event ***g***. Thereby, the proboscis is cleaned off the pollen mass that accumulated amongst the ventral processes during one flower visit and is prepared to collect pollen from the next flower. That pollen would eventually accumulate on the fore tarsi until it is removed and swallowed while the wasp is grooming herself.

Nevertheless, we do not have factual evidence for tarsal pollen transport as we have not found substantial amounts of pollen on the fore tarsi of the collected individuals. On the other hand, dissected individuals contained few if any pollen grains in the glossal sac, probably because the glossa is effectively cleaned either by the fore tarsal brushes or by the maxillae while being retracted.

We have a single observation of "dropmaking" (West-Eberhard 1969) by a female of *C. gestroi*. The individual was resting on a leaf and slowly and repeatedly produced and swallowed back a large drop of liquid which was clear at the beginning, but progressively turned yellow. It is probable that the wasp was producing an important quantity of saliva and moving it back and forth into the mouth cavity and pharynx in order to swallow a large amount of pollen (I.D. Gauld, pers. comm.). Crop, esophagus, pharynx and oral cavity of the dissected females were full of pollen, but it is also probable that some content of the crop was regurgitated while the wasp was dying. Evaporation of excess water is another possibility to explain the "dropmaking" behaviour.

Females build and provision the nest. Dissected females had the crop replete and occupying most of the metasomal volume. The mesenteron itself, on the other hand, though full of pollen, was extremely small, contracted, relegated to a few rear segments of the metasoma together with the proctodeum and the reproductive apparatus. Males had the digestive tract virtually empty, with just a small

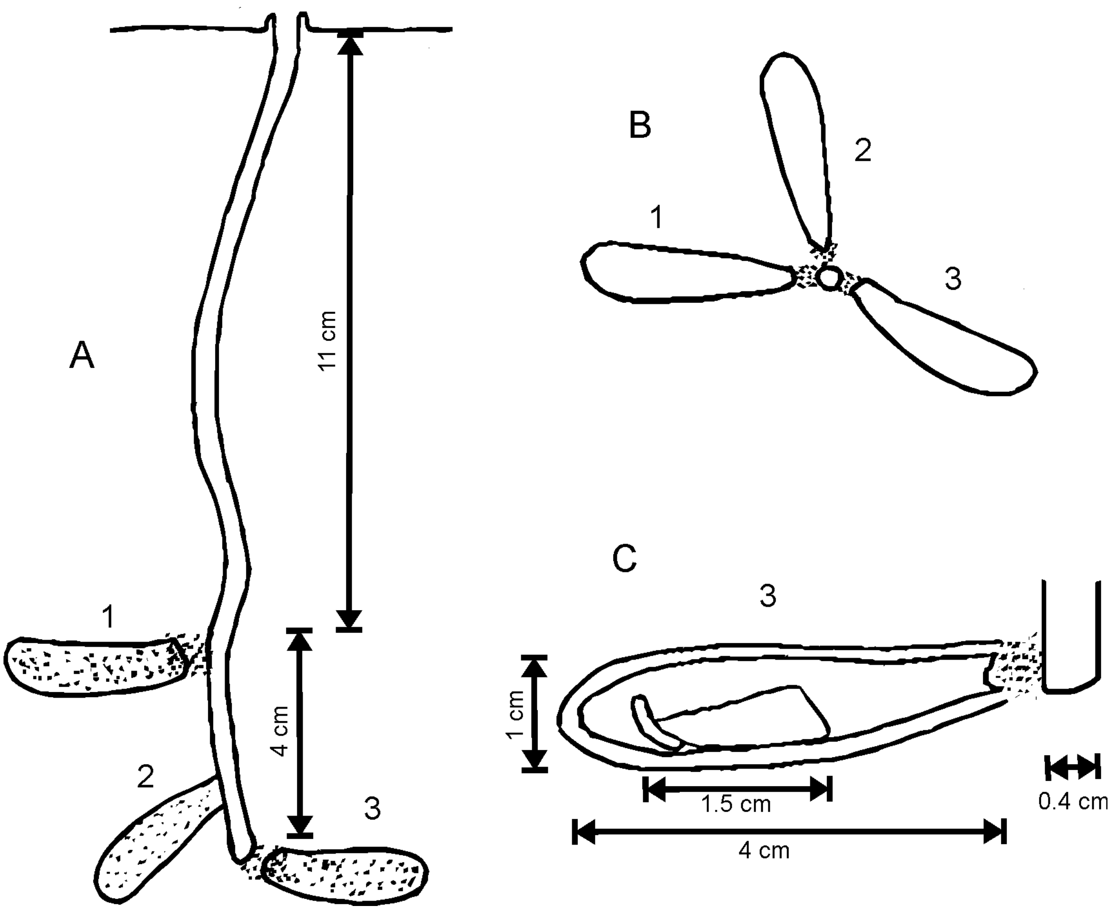

Fig. 4. Nest of *Ceramiopsis paraguayensis* (the numbers indicate the order of depth, 1 for the more superficial one and 3 for the deepest cell). A) Lateral view of the complete nest. B) Orientation of the cells around the main shaft as seen from above. C) Longitudinal section of cell number 3 in lateral view, with the main shaft shown on the right side. The cell was sealed and contained a conical food provision bearing an egg on its bottom-pointing tip.

amount of pollen in the mesenteron. Males probably take more nectar and only little amounts of pollen, in part due to their behaviour but also because they have reduced glossal processes.

Nesting: We were able to locate and dissect only two nests of *C. paraguayensis*. They were both found in an open and sunny spot some 50 meters away from the river bank in the area of Puente Remanso (25°10'57.81"S 57°32'19.74"W). The nests were built underground in flat and compact soil. A third nest, that was not collected, was some 10 meters away from the river bank and was partially hidden by short grass. In the same spot we found nests of at least one unidentified species of bee and of the solitary vespid *Zethus iheringhi* Zavattari. The nest of *Z. iheringhi* differed externally from the nest of *C. paraguayensis* by having a long recurved entrance turret with the opening directing towards the ground.

The following description and the corresponding drawings (Fig. 4) are based on the better preserved nest at the moment of dissecting: The nest consisted of a vertical shaft 4 mm broad and 11 cm deep down to the first cell. The entrance was surmounted by a short earth turret (as described by Bertoni 1921) some 3 mm high. The bottom of the shaft is located some 15 cm under the soil surface, where it ended in front of the sealed entrance of the last cell. There were three cells, located at 11 cm (cell 1), 13.5 cm (cell 2) and 15 cm (cell 3) below the surface respectively. The cells were successively placed clockwise around the vertical shaft. All the cells were sealed. The first cell contained a mature larva inside its cocoon, the next cell an mouldy mass of unrecognizable organic matter and the third cell an egg with its provision. The succession of cell contents indicates that the female built, provisioned and sealed each cell before it started to dig further downwards in order to build the next cell. Each cell was built inside an earth cavity from which it could be easily separated. The cells had an approximately 1 mm thick mud wall. They were finger-like elongated (some 4 cm long by 1 cm wide) and had a concave inner bottom. A plug of agglutinated earth undifferentiated from the surrounding earth separated each cell from the shaft.

The second nest contained four cells, but the structure of the nest and the relative position of the cells could not be reconstructed because the earth piece in which the nest was located suffered severe damage during the extraction. Nevertheless, if we are right about the depth sequence of the cells from top to bottom, their contents were the following: 1) a larva inside its cocoon, 2) a mature larva, 3) a younger larve and 4) an mouldy mass of organic matter.

The provisioned cell (cell number 3 of nest 1) contained a distally pointed conical mass of compact, very solid pale yellow pollen, about 15 mm long and without superficial papillae. The egg was attached to the pointed tip of the provision. Therefore, the egg was probably layed before cell provisioning started, wich is usual in vespids (Carpenter 1982).

The mature larva lined the inner cell walls with a varnish-like secretion before spinning the coccon. The silk cocoon was cylindrical, with the proximal end (facing to the shaft) closed by a perfectly flat rounded lid. The meconium was eliminated inside the cocoon, forming a chain of small yellow cylinders.

CONCLUSION

The Genus *Ceramiopsis* (Hymenoptera: Vespidae: Masarini), is endemic for the Paraguay river basin and comprises two species (*C. gestroi* and *C. paraguayensis*) that are both oligolectic visitors of flowers of the water hyacinth family (Pontederiaceae). Each species is principally restricted by morphology and behaviour to visitin merely one genus of Pontederiaceae. *C. paraguayensis* visits flowers of *Eichornia* (*E. azurea* and *E. crassipes*) while *C. gestroi* prefers flowers of *Pontederia* (*P. cordata* and *P. rotundifolia*), though the latter species has also been observed at flowers of *Eichornia azurea*.

Adult activity is restricted to the hours of higher insolation as usual in most vespids. The flower visiting behaviour is fast and direct, without separate events for nectar and pollen uptake. The very elongated glossal lobes armed with ventral processes help to take up pollen from the lower level anthers hidden deep down into the corolla tube. The fore tarsal brushes help to take up and transfer pollen grains from the glossal lobes to the oral cavity by during grooming movements. The pollen loads are transported by the female in her greatly expansible crop. Males take very little food in their adult life, show a rather feeble territorial behaviour and their mating behaviour is aggressive.

The nest is built in open sunny places with flat compact soil. It consists of a multicellular burrow with a vertical shaft surmounted by a short turret at the entrance. Each cell is a mud capsule built inside an excavated alveole. The cell provision is rather dry and the egg is attached to the distal end of the provision, not to the cell wall. Each cell is built, oviposited, provisioned and sealed by the female before she starts to extend the shaft and in the following to build an additional nest cell deeper inside the ground.

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