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NOTES ON THE TAXONOMY AND ECOLOGY OF THE GENUS HOYA (ASCLEPIADACEAE) IN CENTRAL SULAWESI

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SUMMARY

The taxonomy and ecology of the genus *Hoya* R.Br. are unclear, especially in the core area of its distribution: Sumatra, Borneo, Sulawesi and Irian Jaya. This paper summarises the available information on the ecology of *Hoya* species, and describes eight species from central Sulawesi. An important ecological trait of many *Hoya* species is their association with ants. Four types of mutualistic relationships with ants occur in the genus: 1) species with specialised leaves to house ants; 2) a single species that provides housing for ants under imbricate leaves; 3) species growing on the carton of ant nests; and 4) species that root in ant inhabited cavities in tree trunks and branches. Four of the eight described species grew in association with ants (types 2–4). Taxonomically, *Hoya sussuela* (Roxb.) Merr. is placed in synonymy with *H. coronaria* Blume, and *H. maxima* (H. Karst.) Warb. and *H. pseudomaxima* Koord. are reduced to *H. imbricata* Decne. Three new species are described.

Key words: *Hoya*, Marsdenieae, Sulawesi, ant gardens, ant plants, epiphytes.

INTRODUCTION

The genus *Hoya* R.Br. (Asclepiadaceae: Marsdenieae) consists of an estimated 200 to 300, predominantly epiphytically growing species. Its geographical distribution ranges from S China in the north, the western Ghats (India) in the west, the north Australian rain forests in the south and the Fiji Islands in the east, which corresponds rather accurately with the distribution of rain forests in SE Asia (Richards, 1996). Most species are vines with slender twining stems and typically two opposite leaves at each node. All species have petioled leaves with entire margins. Other than that, variety abounds in the size and shape of organs. The highest species diversity can probably be found in the Indonesian archipelago and directly bordering areas.

The taxonomic description of the genus *Hoya* is at best fragmentary. Significant contributions were made by Schlechter (1913) for New Guinea, Backer & Bakhuizen van den Brink f. (1965) for Java, Rintz (1978) for Malaysia and Forster & Liddle (1990, 1992, 1993, 1995) for Australia and Papua New Guinea. Most contributions of other authors are of one or a few species. The geographical range of *Hoya* is large and split up in numerous countries that used to be rather isolated scientifically. This resulted in many species being described more than once. Furthermore, Rintz (1978) noted

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that numerous species that were mentioned in the literature could not be found in the various herbaria he visited, making the correct identification of specimens difficult. Presently, more than 400 species have been described in this genus (Omlor, 1997) which probably does not contain more than 300, many yet undiscovered, species. Additionally, the large number of synonyms may be caused by the large size and taxonomical complexity of the genus. Both delimitation of the genus within the family and subdivision of the genus into well-defined sections (e.g. see attempts by Burton, 1985 and Kloppenburg, 1994) are still unsatisfactory (Omlor, 1997); only the sections *Eriostemma* Schltr. and *Acanthostemma* (Blume) Koord. are relatively unambiguous. This confusion may be due partly to the haphazard way in which the species have been described, as well as the under-representation of large areas in the heart of the geographical range (e.g. Irian Jaya, Borneo, Sulawesi, Sumatra).

Information on the ecology of all but a few *Hoya* species is limited to the habitat where they were found. Basic ecological data on, for instance, pollinators, flowering rhythm, seed set, pests, diseases, or growth limiting factors are completely absent.

This paper is the first of a series of papers aimed at increasing our knowledge of the taxonomy and ecology of members of the genus *Hoya* in the core area of their distribution. It gives a concise summary of the morphological characters relevant to the description of species. It summarises the available ecological knowledge of the genus supplemented with some novel observations made in central Sulawesi and finalises by describing eight species from central Sulawesi.

MORPHOLOGY

Vegetative growth

Most species of *Hoya* are vines that twine counter-clockwise and produce randomly spaced adventitious roots with which they adhere to their substrate. Some species grow as arboreal shrubs (e.g. *H. multiflora* Blume) or have branches that just hang down from their substrate (*H. cummingiana* Decne.). All but one species produce two oppositely positioned leaves on each node, the exception being *H. imbricata* Decne. that develops only one adult imbricate leave per node (Fig. 8e). Leaf shape of different species range from orbicular (*H. curtisii* King & Gamble) to linear (*H. linearis* Wall.) and may display all levels of hairiness between glabrous (*H. camphorifolia* Warb.) and densely hirsute (*H. parvifolia* Schltr.). Average leaf size of different species is extremely variable but usually somewhere between 0.5 cm (*H. microphylla* Schltr.) and 30 cm (*H. macrophylla* Blume), however, even within species or individual plants leaf size is enormously variable. Leaf venation is usually pinnate (*H. lacunosa* Blume), 3–5-nerved (*H. cinnamomifolia* Hook.), 5–7-nerved (*H. purpureo-fusca* Hook.), or may be obscure in species with more succulent leaves (*H. diversifolia* Blume). Thickness of the leaves varies between herbaceous (*H. multiflora*) to extremely succulent (*H. australis* R.Br. ex Trail subsp. *rupicola* (Hill) P.I. Forst. & Liddle) but, like leaf size, this may vary considerably with the environmental conditions a plant experiences. Flowers are arranged in umbels on persisting peduncles that are positioned on the nodes (a small number of species have peduncles that drop off after flowering). The shape of the peduncle is variable between species but rather constant within species across environments making it a character by which otherwise similar species may be separated when they are not flowering. The umbels may be concave and positively geotropic, convex and positively geotropic, or convex and negatively geotropic, and this is an important taxonomic character (Rintz, 1978) that is particularly helpful in separating two sections from the rest of the genus (section *Acanthostemma* (Blume) Koord. which is characterised by concave, positively geotropic umbels and bilobed coronal extensions (see Fig. 1) and section *Otostemma* (Blume) Miq., also with concave, positively geotropic umbels but with solid outer coronal lobes). The maximum number of flowers per inflorescence varies considerably between species but the number of flowers produced by a single plant depends upon the growing conditions (Forster & Liddle, 1991) which makes it a confusing trait for taxonomic purposes.

As many *Hoya* species flower rarely or infrequently, and numerous herbarium sheets lack flowers, many attempts have been made to distinguish species based on vegetative characters. We find peduncle shape, leaf venation and leaf shape to be the most reliable vegetative characters, while pubescence, leaf size and thickness are generally unreliable. Note however that some species are simply indistinguishable until they flower.

Flowers

The flowers of the Asclepiadaceae are the most elaborate, complicated flowers of all the dicots (Endress, 1994). Organisation and function of Asclepiad flowers have been described in detail by Kunze (e.g. 1990, 1991, 1993), and we therefore refrain from an elaborate description of the *Hoya* flower. An example of a *Hoya* flower with the most important morphological features is given in Fig. 1.

According to Schlechter (1913) and Omlor (1997) the most distinct floral character that separates *Hoya* and the closely related monospecific genera *Absolmsia* Kuntze and *Micholitzia* N.E.Br. from other related genera within the Asclepiadaceae is the shape of the pollinia. *Hoya* pollinia have wings that function as lateral germination fields. However, a considerable number of species within the genus do not have this trait (e.g. all species of the section *Eriostemma* Schltr., *H. darwinii* Loher). Thus a number of different traits are probably required to clearly separate this genus from related genera. The shape of the pollinaria is an important character for taxon delimitation within the genus. It has the additional benefit that the shape of this organ is preserved even in dried flowers (Rintz, 1978). The shape of the corona, corolla, anther wings, and anther appendages are further important taxonomic characters. Flower size is extremely variable, most notably corolla lobe length and width and pollinium length and width (Forster & Liddle, 1991). Size of the flower organs may therefore not be used too rigidly in separating different taxa. The same applies to flower colour which may vary even between the successive flowers on the same peduncle.

Fruits and seeds

Hoya species have two ovaries. However, after fertilisation usually one grows out into a follicle, although the development of two follicles per flower is not very uncommon. *Hoya* follicles are generally long, slim, have a thin pericarp and contain tightly packed, comose seeds. The follicles of the species from the section *Eriostemma* Schltr. form an exception to the rule, by being thick courgette-like with a spongy pericarp. On maturity, the follicle splits open along a single suture, revealing the long, thin and slightly flattened seeds, apically with the still damp comas (or plumes).

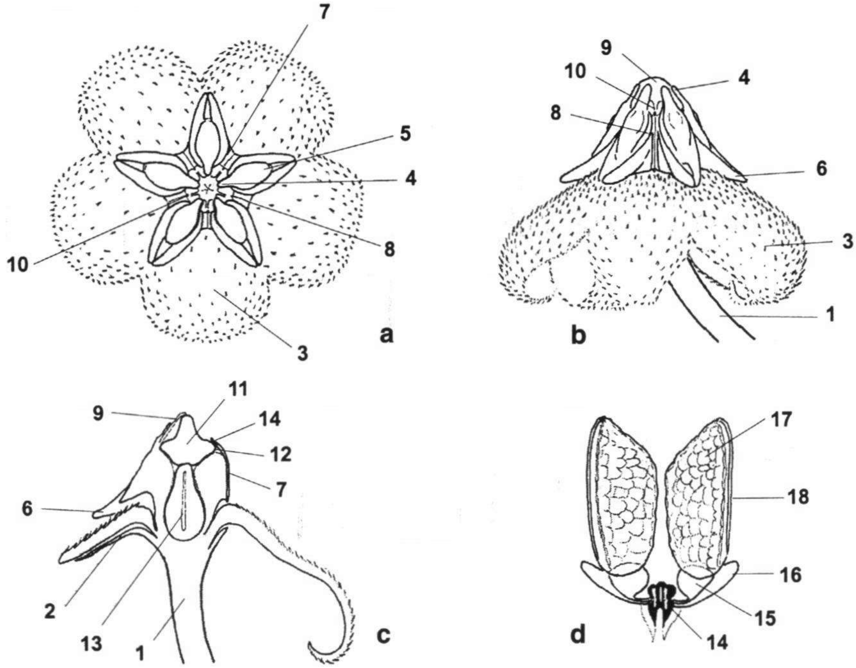

Fig. 1. A flower of the genus *Hoya* (section *Acanthostemma* (Blume) Koord.) showing most of the typical characters. – a. Top view; b. side view; c. median sectional view; d. pollinarium. – 1. Pedicel; 2. calyx; 3. corolla; 4. inner coronal lobe; 5. outer coronal lobe; 6. bilobal coronal extensions; 7. anther wing; 8. guide rail; 9. anther appendage; 10. pollinarium; 11. style head; 12. receptive area of style head; 13. ovary; 14. retinaculum; 15. caudicle; 16. caudicle wing; 17. pollinium; 18. pollinium wing.

As the comas dry, they expand and push the seeds outward and upward until they are caught by the wind and float off (Rintz, 1978). The plume is very hygroscopic which helps the seed to adhere to any damp surface with which it comes into contact, such as the bark of a tree. Seeds germinate immediately upon encountering a moist substrate (Rintz, 1978). Most species set seed rarely. It is therefore not clear what the value is of follicle and seed morphology for taxon delimitation within the genus.

ECOLOGY

Distribution in different habitats

Most *Hoya* species grow between 0 and 800 m altitude. In this zone, they can be found primarily along rivers, lakes and sea shores, usually on the stem and primary and secondary branches of trees. More rarely, specimens of epiphytic species can be found growing on, usually, calcareous but occasionally other types of rock outcrops. The species of the section *Eriostemma* Schltr. all grow terrestrial, which at times may be difficult to notice as they climb into and crawl over nearby shrubs and trees. The more common *Hoya* species also occur regularly in rural areas, growing on roadside, fruit and ornamental trees, in old trees on graveyards and in plantations. Of course, these observations are probably biased by the poor access any observer has to the canopy of primary lowland forests. Sightings of *Hoya* specimens growing in the canopies of 30 m tall solitary trees, left standing after the surrounding forest had been cut down, suggest that this genus does occur in this niche as well. What species do so and how important this niche is in their habitat remains unclear.

The geographical range of a smaller number of *Hoya* species is restricted to higher altitudes. The upper limit is usually between 1200 and 2000 m: ±1500 m in Malaysia (Rintz, 1978), ± 2200 m in New Guinea (Schlechter, 1913), ± 1700 m in Java (Backer & Bakhuizen van den Brink f., 1965) and ± 1200 m in Sulawesi. Presumably because the structure of mountain forests is much more open than lowland forests, *Hoya* species at higher altitudes grow scattered throughout the entire forest and many species can be found growing on a range of substrates, from tree branches heavily covered in moss to cracks in bare granite rock.

Seed dispersal

The plumed seeds of *Hoya* suggest adaptation to wind dispersal. Their potential for long distance dispersal was illustrated on the Krakatau Islands where a primary succession was started after the devastating volcanic eruption of 1883. The first *Hoya* species (re-)colonised the islands between 51 and 68 years after the eruption. In 1979 *H. lacunosa* and *H. diversifolia*, two species that are common on Java and Sumatra (some 30 km distant), were firmly established on respectively two and all three of the Krakatau Islands (Bush et al., 1995). The mode of dispersal of many *Hoya* species may be characterised as diplochorous, that is, two modes of dispersal are involved in the establishment of a new plant. Once they have been dispersed by wind, the seeds of these species are actively collected by ants and placed in their arboreal nests and runways (Docters van Leeuwen, 1929; Kiew & Anthonysamy, 1987). On Java, Docters van Leeuwen (1928) found that the seedcoat of, amongst others, *H. lacunosa*, contained high concentrations of oils. He suggested that this was the main stimulant for ants to collect seeds although it remains unclear why they should plant them in the carton of their nest and runways. Seed dispersal of the numerous *Hoya* species that associate with ants are therefore both anemochorous and myrmecochorous.

Hoya and ants

Many species of *Hoya* grow in association with ants. The particular nature of the relationship varies between species but four general categories can be recognised.

First, *Hoya* species that have myrmecodomatia, or leaves adapted to house ants (Weissflog et al., 1999). *Hoya mitrata* Kerr forms, besides normal leaves, domatia that consists of about five leaf pairs. The tip and margin of the inner-most leaves of the first pair are pressed to the host tree surface, forming a cavity between the bark and the underside of the vaulted leaf. The leaves of the next pairs are pressed in a similar fashion to the leaves of each older pair, covering them partly, ultimately resulting in a multichambered structure. This structure is usually inhabited by ants of a range of genera, many of which were found to be nesting there (Weissflog et al., 1999). Extensive root systems develop only inside the domatia when ants were present depositing organic material in the chambers. *Hoya darwinii* also has dimorphic leaves as a specialisation to the housing of ants. The domatia are spherical and made up of several leaves, tightly pressed together forming a globose pouch with 4–6 cavities (Kloppenburg, 1993).

Second, *Hoya* species with specialised convex-orbicular leaves. *Hoya imbricata* Decne. [syn. *H. maxima* (H. Karst.) Warb., see below] has large imbricate leaves with margins that are tightly pressed against the bark of stems or branches. This species is unique amongst all *Hoya* species in developing only one mature leaf per internode. A succession of such leaves is placed over the stem (Fig. 8e) and roots only develop fully underneath the leaves, which allows the plants to grow on very exposed substrates (Karsten, 1895). The space below each leaf is usually occupied by one of several species of ants. Supposedly, this type of mutualism, which is more commonly observed in the related genus *Dischidia* R.Br. (e.g. *D. albiflora* Griff., *D. astephana* Scort. ex King & Gamble, *D. cochleata* Blume, *D. imbricata* (Blume) Steud., *D. longipedunculata* Ridl.), provides shelter and food in the form of floral nectar for the ants, while the plant benefits from the extra nutrients obtained from the organic material that is collected and deposited underneath the leaves by the ants. Thus far, *H. imbricata* is the only known *Hoya* species with this kind of specialisation.

Third, *Hoya* species that grow on ant nests. This is by far the most common type of relationship. Ant nests are constructed from a variety of materials ranging from plant fibres and thin bark to decaying leaves, sand, soil and organic debris (Wheeler, 1910). Seeds of epiphytes planted in the potentially nutritive ant carton therefore encounter more favourable germination conditions and plants may grow more rapidly (Kleinfeldt, 1978). In the Malesian archipelago, *Hoya* species are usually just one of a set of species that systematically grow on arboreal ant nests. Such 'ant gardens' were first described by Ule (1901) in Brazil. Doctors van Leeuwen (1928) suggested that the overgrown nests of the ant species *Crematogaster baduvi* Forel and a *Iridomyrmex* Mayr species observed by him on Java were the Asian equivalent of the same phenomenon. In his case *H. lacunosa* was usually accompanied by *Dischidia major* (Vahl) Merr., *D. imbricata*, *D. punctata* (Blume) Decne., and the ferns *Lecanopteris curtisii* Baker and *L. sinuosa* (Wall. ex Hook.) Copel. In Sulawesi we found the nests of the ant species *Iridomyrmex cordatus* Fr. Smith to be the substrate of ant gardens which are closely related to the one observed by Docters van Leeuwen (1928) (Fig. 2). Table 1 shows that the primary components of the ant gardens in central Sulawesi were *H. brevialata* spec. nov. (see below), *Dischidia imbricata*, *Dischidia nummularia* R.Br. and the orchid *Dendrobium bicaudatum* Reinw. ex Lindl. while the ferns *Pyrrosia longifolia* (Burm.f.) Morton and *Lecanopteris sinuosa* occurred somewhat less regularly. Interestingly, Table 1 confirms earlier observations by Kiew & Anthonysamy (1987) that the distribution of *Dischidia major*, a classical ant plant with pitcher leaves in which ants may nest, is poorly correlated with the location of ant nests, while species with no obvious adaptations to house ants, such as *H. brevialata* and *Dischidia nummularia* are strongly correlated. *Hoya* species growing on the carton of ant nests have never been observed above approximately 800 m altitude. We speculate that this may be caused by the absence of ants that construct this type of nests as the conspicuous carton ant nests are rarely observed above this altitude; not in Sulawesi nor in any other area in Indonesia visited by the authors. In support of this view are the findings of Huxley (1978) when examining the altitudinal distribution of the ant species *Iridomyrmex cordatus*. In addition to building carton nests this species inhabits the

Fig. 2. A well-developed ant garden in central Sulawesi (Gintu, Bada Valley). A nest of the ants *Iridomyrmex cordatus* overgrown with a number of typical epiphytes: ***Asplenium nidus*, *Dendrobium bicaudatum*, *Hoya brevialata*, *Lecanopteris sinuosa*** and ***Pyrrosia piloselloides*.**

cavities in most SE Asian ant plants (e.g. Janzen, 1974). However, while she found *I. cordatus* to be the most common occupant of ant plants of the genera *Hydnophytum* Jack and *Myrmecodia* Jack in lowland forests, she found it to be absent in upper montane forests where it was replaced by another *Iridomyrmex* species, suggesting that it is restricted to lower altitudes. In contrast to ant garden epiphytes, epiphytes that provide housing for ants are common at high altitudes, for instance species of *Hydnophytum* and *Myrmecodia* were found at 2400 m in New Guinea (Huxley, 1978) or *Lecanopteris spinosa* Jermy & Walker at 1950 m in central Sulawesi (Jermy & Walker, 1975). *Hoya* species that are commonly found on ant nests are: *H. lacunosa*, *H. brevialata*, *H. parvifolia*, *H. pubera* Blume, *H. picta* Miq., *H.* spec. *IPPS 4562* from Biak. However, the ecological characteristics of most *Hoya* species are unknown and we expect that many other species, especially from the section *Acanthostemma* (Blume) Koord., demonstrate this type of relationship with ants.

Table 1. Plant species found on the arboreal nests of *Iridomyrmex cordatus* ants around Tentena (no. 1–11) and Gimpu (Bada Valley, no. 12–21) in central Sulawesi.
* = substrate bamboo; ** = substrate bare rock; T = Total.

Ant nest no.: species	1	2	3	4	5	6	7	8	9	10	11	12	13	14*	15	16*	17	18	19	20	21**	T
Hoya brevialata	•	•	•	•	•	•	•		•	•		•	•	•	•	•	•	•	•	•		18
Dischidia nummularia	•		•	•		•		•	•		•	•	•	•	•	•	•	•	•	•		16
Dendrobium bicaudatum		•		•	•		•		•			•	•		•	•	•	•	•	•		13
Dischidia imbricata		•		•	•	•	•	•			•		•	•			•		•	•	•	13
Pyrrosia longifolia				•	•		•		•						•				•	•	•	8
Lecanopteris sinuosa												•	•			•		•	•	•	•	7
Pyrrosia piloselloides	•	•					•					•										4
Myrmecodia spec.															•			•		•		3
Asplenium nides L.												•										1
Dischidia major		•																				1
Dischidia spec.			•																			1
Drynaria sparsisora (Desv.) T. Moore							•															1
Phymatosorus scolopendrius (Burm.f.) Pic.Serm.							•															1

Fourth, species growing in ant inhabited cavities in tree trunks and branches. In central Sulawesi, *H. myrmecopa* spec. nov. (see below), was found growing from little holes in tree branches (Fig. 10e), resembling the growth habit of parasitic species. Closer inspection learned that the root system of the plant was growing in a number of connected cavities that served as a nest site of ants of the genus *Tetramorium* Mayr. *Hoya pallilimba* spec. nov. (see below) was found growing in a similar fashion from a little circular hole in a hollow *Pandanus* spec. root (Fig. 11e). The hole was closed with ant carton, however, ants were absent at the time of observation. Weir & Kiew (1986) reported a similar relationship between ants of the genus *Crematogaster* Lund and the epiphytes *Dischidia astephana* and *D. parvifolia* Ridl. in Malaysia. They found that trunks and branches of the tree *Leptospermum flavescens* Sm. contained interconnected cavities (irrespective of the presence of the ants) that housed a single colony of the ants. Little holes were used by the ants to reach the surface of the branches and by the roots of both species of *Dischidia* to penetrate the central cavities in the branches where they occupied a substantial volume of the available space. Green (1993) observed *Absolmsia spartioides* (Benth.) Kuntze growing in a similar fashion from holes in the stems of trees with their main root system within the rotted out centre of trunks that were 7.5–10 cm in diameter. Thus, this type of ant-epiphyte relationship may be quite common under epiphytic Asclepiads but may often have been overlooked in the past due to its inconspicuousness. Of both *Hoya* species from Sulawesi (almost) the entire root system of the plants was confined to the cavities, suggesting that collection of the seeds by the ants and transport into their nests is the basic mechanism that gives rise to this relationship. However, both *Hoya* species were also observed growing outside ant-inhabited structures, supporting the general view that the epiphytes are essentially the scavengers on the ant-tree relationship (Weir & Kiew, 1986). Thus far, *H. myrmecopa* and *H. pallilimba* are the only known species within the genus that demonstrate this type of relationship with ants.

Pollination

The pollinators of all but one *Hoya* species remain unknown. Forster (1992) found that *H. australis* R.Br. ex Traill was effectively pollinated by *Ocybadistes walkeri sothis* Waterhouse (Lepidoptera: Hesperiidae), a day flying butterfly. The flowers of most *Hoya* species open at dusk however, which, combined with the fact that the dominant flower colours are white, greenish or pale yellow, suggests that nocturnal insects play an important role in the pollination process. The study of Forster (1992) did not exclude the possibility that night flying insects were partly responsible for the observed pollination efficiency. The richly produced nectar and the strong scent of the flowers at night are the main incentives respectively attractants for the pollinators. Altenburger & Matile (1988) experimentally determined for *H. carnosa* R.Br. that fragrance is emitted in a circadian rhythm, that is, flowers timed their emission of fragrance to occur c. 12 hours after the last dark period, so that the next emission would again fall in a dark period. Nectar may also play an important role in the relationship between *Hoya* species and ants. Ants can be seen scurrying incessantly on the flowers of *Hoya* species, feeding on the nectar. In addition to the oils in the cuticular cells of the seeds, the copious nectar produced by *Hoya* species may be a strong incentive for the ants to plant seeds of these species in the carton of their nests. It is doubtful whether ants play a role in the pollination of these species, as was originally suggested by Schlechter (1916). Ants are considered to be poor pollinators. In contrast to juvenile stages of the related bees and wasps, that are protected by nests of wax or paper respectively, juvenile stages of ants lie relatively exposed to attacks from microorganisms (Beattie, 1985). It is suggested that ants cover themselves and their broods with antibiotics that incidentally inhibits pollen growth. This may have presented a barrier to the evolution of ant pollination systems (Beattie, 1985). On the other hand, pollen in the genus *Hoya* is released in pollinaria, which may make them less susceptible to damage. Beattie (1985) notes that some of the species that were reported to be ant pollinated were orchids, that, like *Hoya* species, deposit pollen as pollinia.

Conservation

The main threat to species of the genus *Hoya* is habitat destruction. Being epiphytes, they are even more susceptible to logging and clear-cutting than terrestrial rain forest species. Many species show a particular preference for trees of a minimum size, for moss-covered branches or are co-inhabitants of hollows in tree branches occupied by ants. It may take a long time before a suitable substrate has developed after a major disturbance, if natural regeneration is allowed to proceed at all. Such species face a high extinction threat and many species may have disappeared already. Most species are easy to grow in situ; however, they have low appeal to the local population. Unlike orchids which are being collected and placed on garden trees by most local people, we have seen only once a *Hoya* species (*H. diversifolia* in E Java) that was used as an ornamental plant. Conservation of these species depends therefore on the conservation of the forests in which they grow.

Fortunately, other species are more robust and may be encountered regularly in rural and even urban areas. For instance, *H. diversifolia* grows on the large *Ficus* trees that adorn the main squares ('alun-alun') of large cities such as Medan (Sumatra) or Malang (E Java). Such species will probably survive most alterations imposed by man on their habitat for a long time.

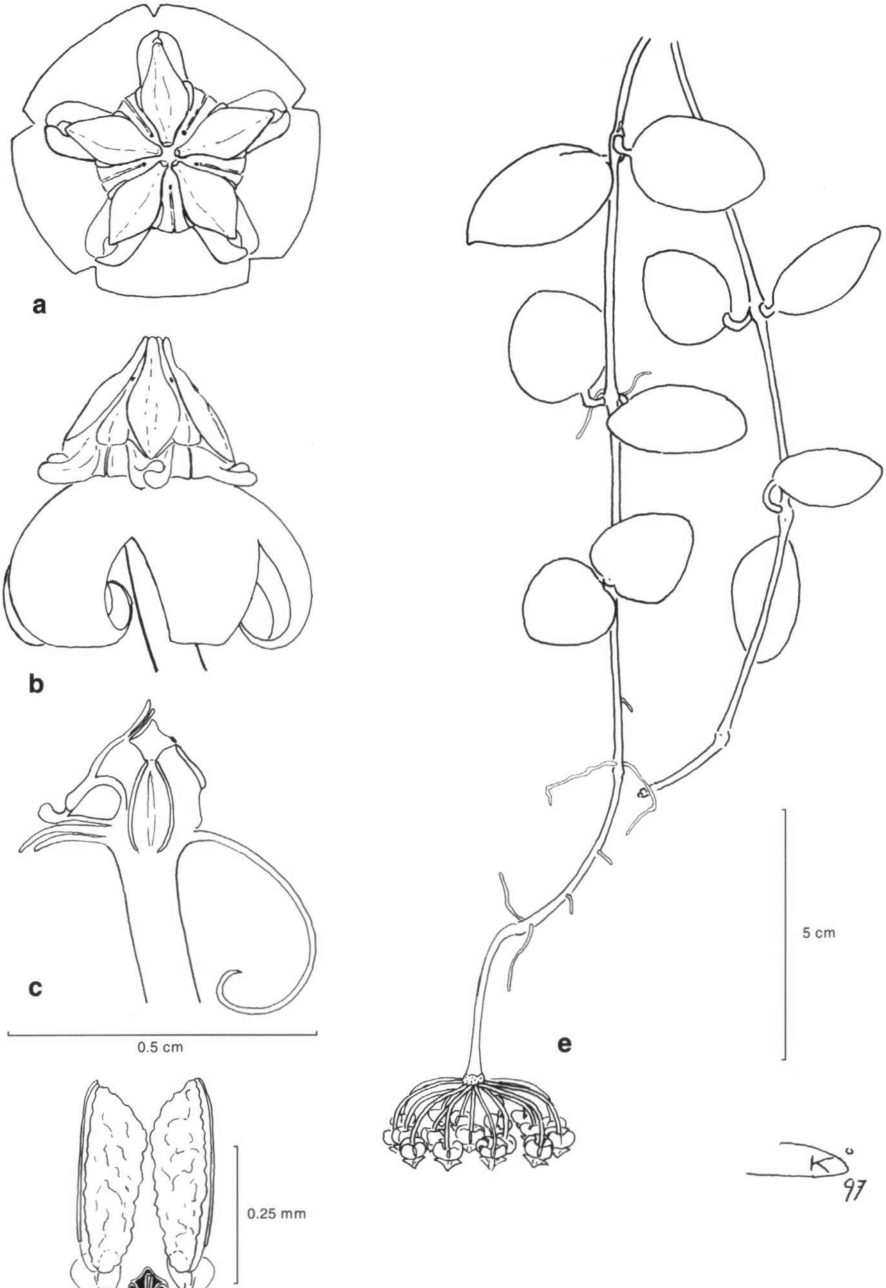

Fig. 3. *Hoya brevialata* Kleijn & Van Donkelaar. a. Flower in top view; b. flower in side view; c. flower in median section; d. pollinaria; e. growth habit (drawn from live material grown indoors in the Netherlands; *IPPS 7718*).

HOYA SPECIES IN CENTRAL SULAWESI

We estimate that the total number of *Hoya* species in Sulawesi will be between 15 and 20. We have observed 13 distinct species. This number is based partly on examination of both vegetative and generative characters and partly on vegetative characters only as not all species were seen flowering. The eight species that were observed flowering are described in detail below.

1. **Hoya brevialata** Kleijn & Van Donkelaar, *spec. nov.* — Fig. 3

> Caules tenues glabrescentes internodiis brevibus. Folia suborbicularia ad elliptica pallide viridia vel flavida ad clare rubra ubi exposita. Petioli 0.5–1 cm longi. Pedunculi 3–6 cm longi. Umbellulae concavae positive geotropicae floribus 15–25. Florum colores a fere albi ad profunde rubri variantes, corona plerumque corolla aliquantum gradus rubriores lobis supra cristatis extensionibus bilobatis manifeste sursum curvatis, corolla valde recurvata utrinque glabra. Antherae alae proprie breves gynostegii ad dimidio attingentes (Fig. 3b, c), caudiculis angustis pyriformibus alatis. — Typus: *Kleijn & Van Donkelaar IPPS 8836* (holo L), Indonesia, C Sulawesi Province: Tentena, in clove plantation.

Stems thin, glabrescent, with short internodes. *Leaves* suborbicular to elliptic, light green, yellowish to bright red when very exposed. *Petioles* 0.5–1 cm long. *Peduncles* 3–6 cm. *Umbels* concave, positively geotropic, with 15–25 flowers. *Flowers*: colour ranging from almost white to deep red, corona usually one to several shades darker than corolla, upper side of the coronal lobes ridged, bilobal extensions clearly upcurved, corolla strongly recurved, glabrous on both sides. *Pollinaria* anther wings characteristically short, coming down only halfway the gynostegium (Fig. 3b, c), caudicles narrow with pear-shaped wings.

Distribution — *Hoya brevialata* is only recorded from Sulawesi.

Ecology — From 0 to 600 m altitude, *H. brevialata* is by far the most conspicuous species in central Sulawesi probably due to the fact that it is especially abundant in rural and semi-natural habitats. *Hoya brevialata* often grows in association with ants (usually *Iridomyrmex cordatus*, Fig. 2, Table 1), apparently starting growth from the ant nests but subsequently colonising the entire tree. It also grows without ants, simply attached with adventitious roots to the bark of tree trunks, or literally draped through the crown of ornamental and fruit trees in gardens, in clove tree plantations and in roadside trees. In natural habitats it is less conspicuous but also quite common, especially along shores of rivers, lakes and seas using a variety of trees of all sizes and shapes as substrate.

Note — The name *H. brevialata* refers to the typically short anther wings, 'short' being 'brevis' and 'wing' being 'ala' in Latin.

2. **Hoya camphorifolia** Warb. — Fig. 4

Hoya camphorifolia Warb., in Schltr. & Warb. in Perkins, Fragm. Fl. Philipp. 1 (1904) 129. — Type: *Warburg s.n.* (B, now lost), Philippines, Luzon, Tayabas Province, Sampaloc.

Leaves oblong to elliptic, shortly accuminate, glabrous with usually three conspicuous whitish main veins. *Petioles* glabrous, 1–2 cm long, thicker than the stems. *Peduncles* characteristically long (5–11 cm), very thin. *Umbels* convex, negatively geotropic,

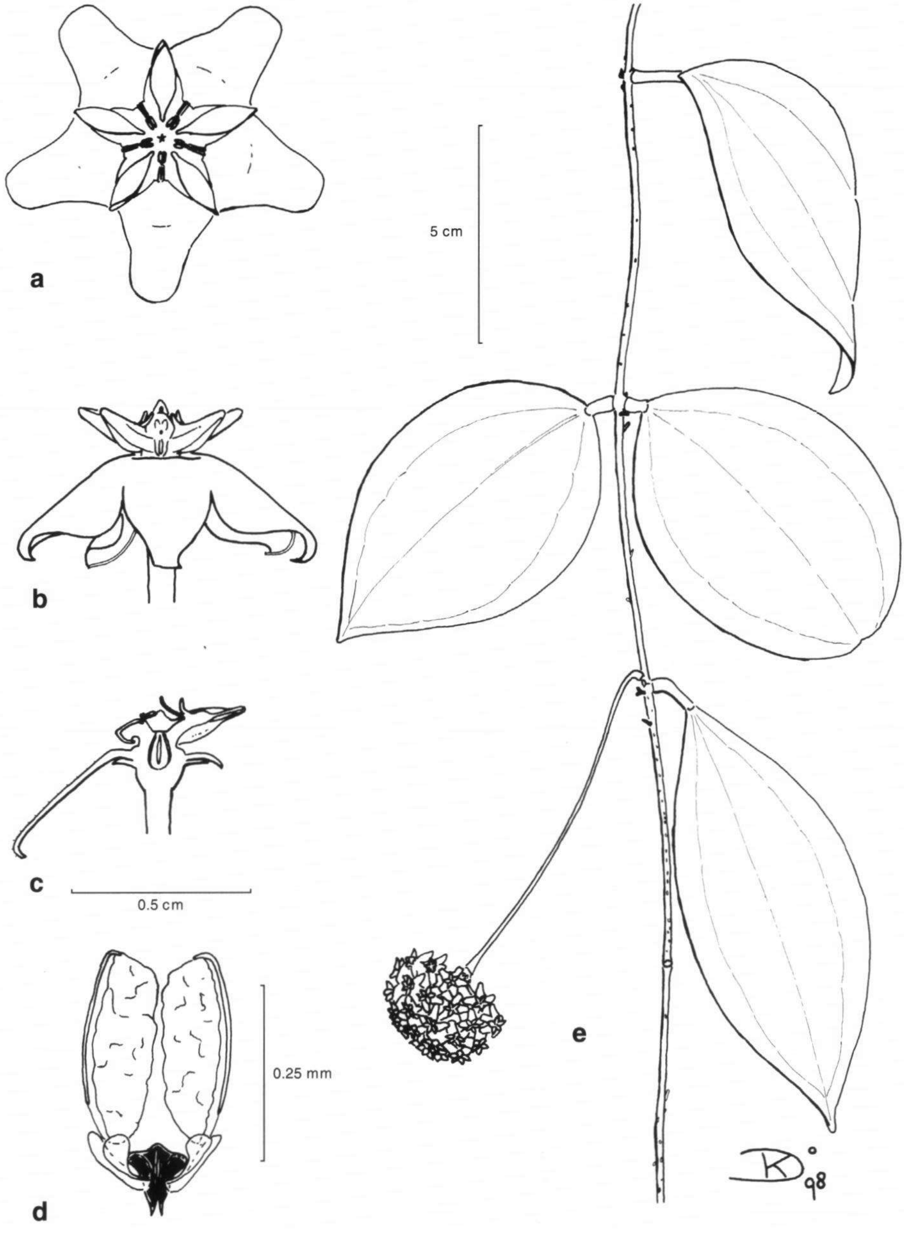

Fig. 4. *Hoya camphorifolia* Warb. a. Flower in top view; b. flower in side view; c. flower in median section; d. pollinaria; e. growth habit (drawn from live material grown indoors in the Netherlands; *IPPS 8845*).

with 20–40 flowers. *Flowers* whitish pink to purplish, the corona darker than the corolla, open for one day only; coronal lobes lanceolate, upper sides concave, lower sides with broad grooves, outer coronal lobe tips higher than inner coronal lobe tips; corolla faintly pubescent, lobes recurved. *Pollinaria* retinaculum short and thick, broadly flat top tapering off about exponentially to narrow bottom tip; caudicles narrowly winged.

Distribution — This species was originally described from the northern Philippines and has not before been recorded for Sulawesi. The species is probably common throughout the Philippine archipelago and Sulawesi.

Ecology — *Hoya camphorifolia* may be seen growing as dangling masses of stems hanging from the primary branches of trees, but equally often these scramble through undergrowth or shrubs. Even more than other species in the genus, old and young plant parts of *H. camphorifolia* have a distinct appearance. The stems become woody and increase considerably in thickness with age. Young leaves are dark green and coriaceous, but they usually turn pale green and become highly succulent with age. *Hoya camphorifolia* is common from 0–600 m altitude. It is very abundant on the seashore growing in bushes on rock outcrop or on flood plains just behind the mangrove forests in trees and *Pandanus* palms. It is also regularly found in more anthropogenic environments, hanging from large trees between sawahs or growing in shrubs bordering plantations. No association was observed with ants despite Elmer's (1938) observation in the Philippines that this species grew from an ant nest.

Note — The Sulawesi specimens have narrower coronal lobes than the Philippine plants and have recurved corolla lobes while their Philippine counterparts have more or less flat corolla lobes. Otherwise the plants from both areas are similar.

3. Hoya coronaria Blume — Fig. 5, 6

Hoya coronaria Blume, Bijdr. 16 (1827) 1063. — Types: *Blume s.n.* (lecto L, no. 898.168-121, designated here), *Blume s.n.* (iso L, no. 898.168-128), Java.

[*Coronaria ariadnes punicea* Rumph., Herb. Amboin. 5 (1750) 464, t. 172.] — *Asclepias sussuela* Roxb., Fl. Ind. ed. 2 (1832) 31. — *Hoya ariadna* Decne. in A.DC., Prodr. 8 (1844) 635. — *Hoya corona-ariadnes* Blume, Rumphia 4 (1849) 31. — *Hoya sussuela* (Roxb.) Merr., Interpr. Herb. Amboin. (1917) 438. — Syntypes: Rumph., Herb. Amboin. 5 (1750) t. 172, *Roxburgh s. n.* (possibly in BM).

Hoya velutina Wight, Contr. Bot. Ind. (1834) 35. — Type: Contr. Bot. Ind. (1834) t. 8150.

Hoya grandiflora Blume ex Decne. in A.DC., Prodr. 8 (1844) 635. — Type: *Blume s.n.* (lecto L, no. 898.168-123, designated here).

Hoya speciosa Decne. in A.DC., Prodr. 8 (1844) 634. — Type: *Labillardière s.n.* (holo P n.v.), Amboina.

Hoya coronaria Blume var. *papuana* F.M. Bailey, Queensland Agric. J. 3 (1898) 156. — Type: *F.M. Bailey AQ360787* (holo BRI n.v.), Papua New Guinea, N Prov., foot of Mt Trafalgar (= Mt Iamiwara).

Hoya hollrungii Warb., Feddes Repert. Spec. Nov. Regni Veg. 3 (1907) 342. — Type: *Hollrung 661* (B, now lost), Papua New Guinea, W Sepik (= Sundaun) Province, Augusta Station, 1887.

Stems thick, densely hirsute. *Leaves* oblong, base obtuse-rounded, shortly accuminate from a broadly rounded or slightly narrowed top, thickly coriaceous, with a strong midrib and less pronounced side nerves. *Petioles* short, hairy, 1–2 cm long. *Peduncles* short, thick, pubescent. *Umbels* convex, negatively geotropic, with a small number of very large flowers. *Flowers*: coronal lobes yellowish white, usually positioned in a

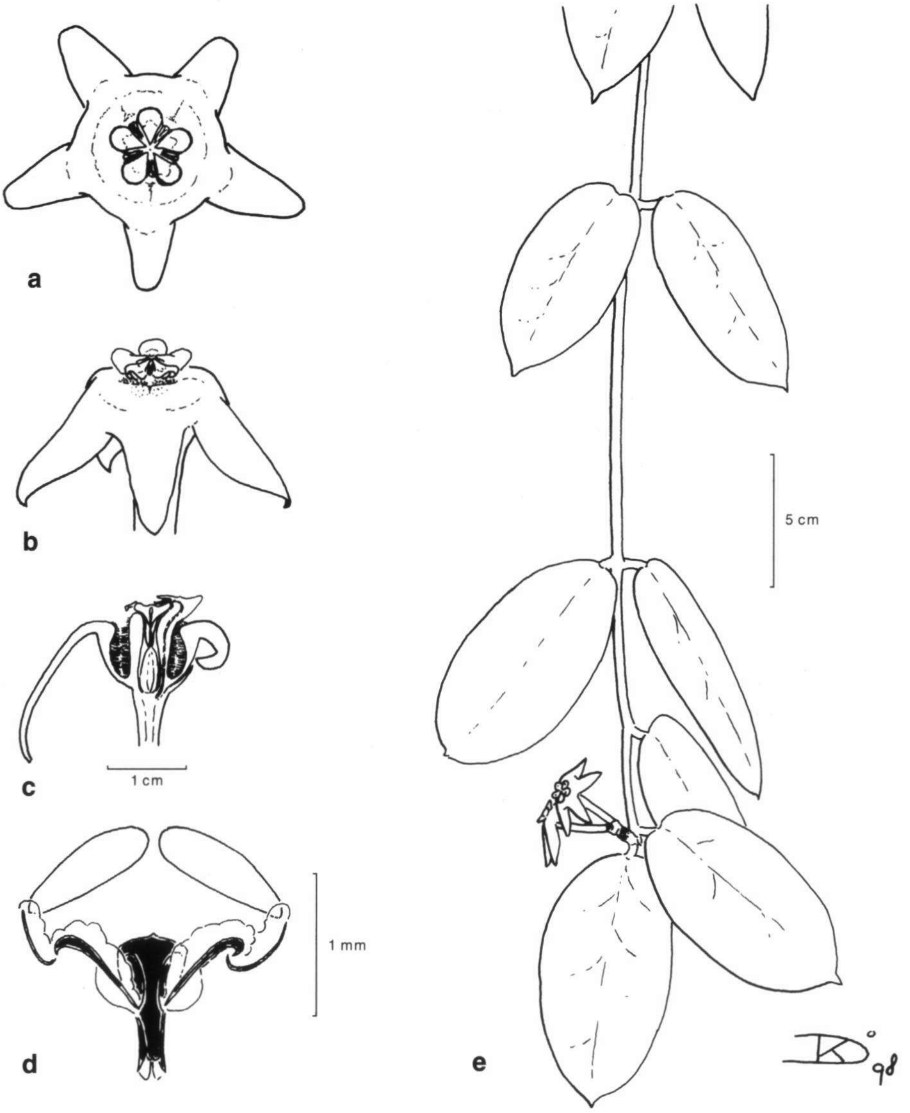

Fig. 5. *Hoya coronaria* Blume. a. Flower in top view; b. flower in side view; c. flower in median section; d. pollinaria; e. growth habit (drawn from a plant growing on the north-eastern shore of Lake Poso; *IPPS 8891*).

horizontal plane although in some specimens the outer coronal lobe tips are somewhat elevated, inner coronal lobes acute, outer coronal lobes obtuse-rounded; corolla varying from slightly campanulate, patent to stellar, usually yellowish white or reddish yellow often violet dotted. *Pollinaria* retinaculum pear-shaped with tip on the upper broad side, caudicles made of two segments of a dark secreted material connected by a transparent membrane attached laterally over the entire length of the dark segments, pollinia wingless.

Distribution — *Hoya coronaria* has an extremely wide range and can be found in northern Australia, Papua New Guinea, throughout the Indonesian archipelago and in Peninsular Malaysia. It is unclear whether it also occurs in the Philippines.

Ecology — *Hoya coronaria* grows terrestrially. It may climb high into trees and shrubs but may also grow amongst herbaceous vegetation on the ground. It is extremely common in central Sulawesi between 0 and 800 m altitude, especially along the shores of rivers and lakes, in roadsides and occasionally in remnants of disturbed natural vegetation in agricultural areas.

Notes — Examination of the literature (e.g. Rintz, 1978; Forster & Liddle, 1992) and herbarium sheets showed that two species from the section *Eriostemma* were described for Sulawesi, *H. coronaria* and *H. sussuela*. We found only one, very common species of this section, and therefore compared our specimen with the types of both species. Although some differences could be found in shape of corona and corolla (in central Sulawesi only reddish yellow, stellar flowers have been observed), overall our specimen resembled both types. A comparison of our plate (Fig. 5, Sulawesi) with the plates drawn by Rintz (1978; *H. coronaria*, Malaysia), Forster & Liddle (1992; *H. sussuela*, Australia), those in table 182 and 184 by Blume (Blume, Rumphia 4, 1849; *H. sussuela*, Moluccas), and pickled material from Sumatra (*H. coronaria, IPPS 7023*) showed that, although the flowers varied somewhat (particularly in corolla colour and shape: from stellar to almost campanulate), overall differences were not significant. Especially the shape of the pollinaria is very constant in specimens over the whole geographical range. For comparison, pollinaria of the Sulawesi specimen, the above mentioned Sumatra specimen, *H. ciliata* Elmer ex Burton from the Philippines, and an unidentified *Eriostemma* Schltr. species from Biak, Irian Jaya are given in Fig. 6.

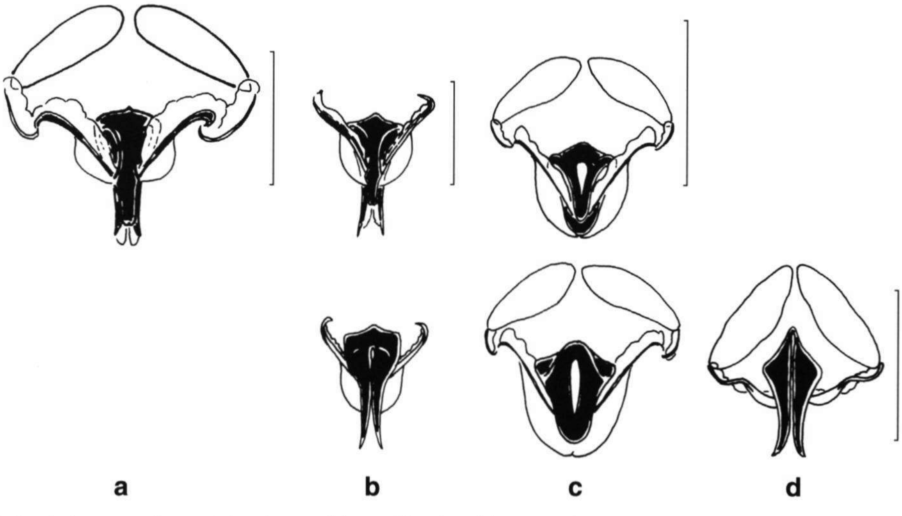

Fig. 6. A comparison of the shape of the pollinaria of four specimens of section *Eriostemma* Schltr. from different geographical locations. a. *Hoya coronaria* from central Sulawesi, bottom side; b. *H. coronaria* from Aceh Province, Sumatra (pollinia lost), top: lower side, bottom: upper side; c. *H. ciliata* from the Philippines, top: lower side, bottom: upper side; d. unidentified *Hoya* species from Biak, Irian Jaya, upper side. — All scale bars 1 mm.

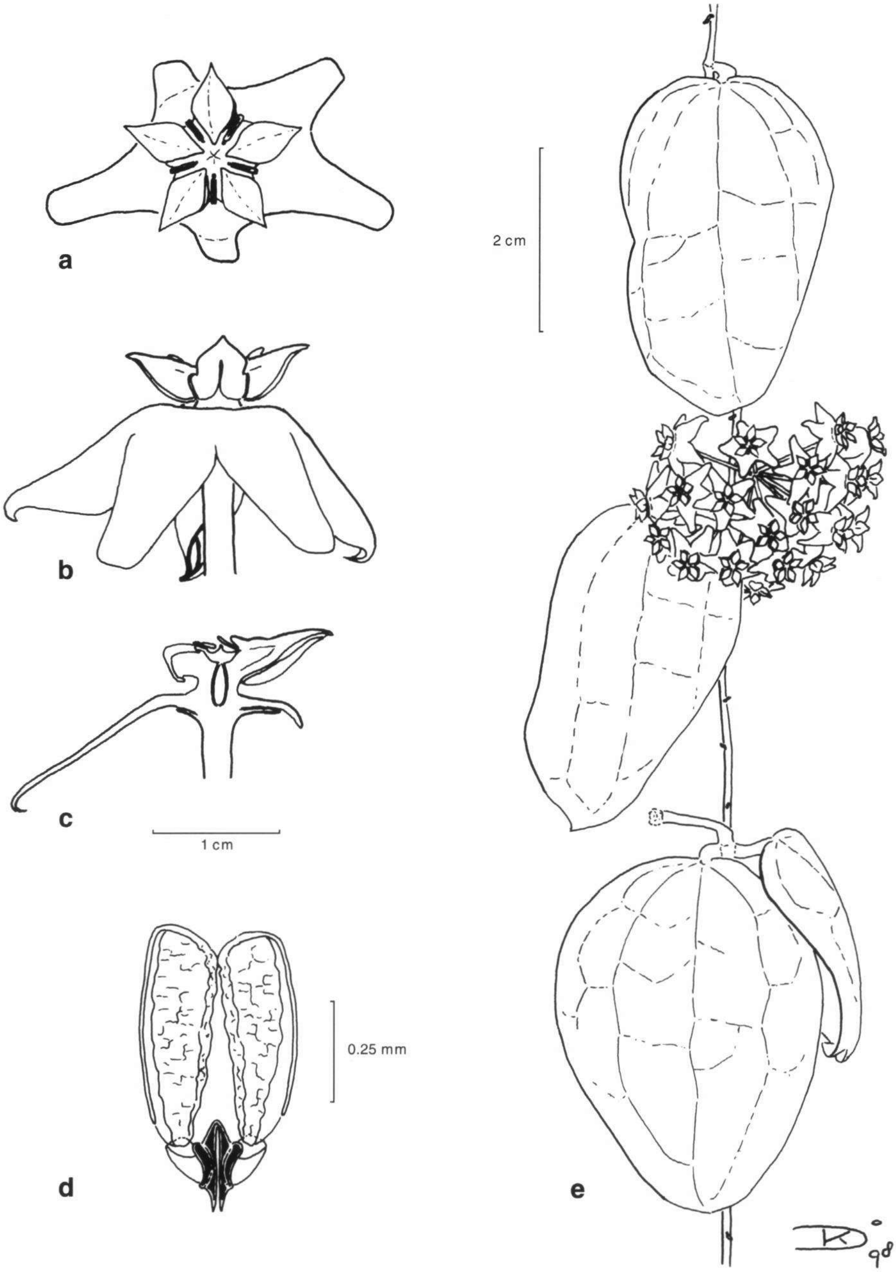

Fig. 7. *Hoya dolichosparte* Schltr. a. Flower in top view; b. flower in side view; c. flower in median section; d. pollinaria; e. growth habit (drawn from live material grown indoors in the Netherlands; *IPPS 8831*).

In particular the retinacula of the Philippine and Biak species differ from the Sulawesi and the Sumatra specimens as well as from one another. By contrast, the retinacula of the Sulawesi and Sumatra specimens are nearly identical. We therefore conclude that *H. coronaria* and *H. sussuela* are synonyms and place *H. sussuela* in synonymy with *H. coronaria.*

4. Hoya dolichosparte Schltr. — Fig. 7

Hoya dolichosparte Schltr., Beih. Bot. Centralbl. 34, 2 (1916) 13. — Type: *Schlechter 20642* (holo B), Indonesia, C Sulawesi Province: Toli-Toli.

Stems thin, lignify quickly with age, pocked with short adventitious roots. *Leaves* ovate with conspicuous light venation, 3–5 main veins connected by numerous side veins. *Petioles* thick, 1–2 cm long. *Peduncles* characteristically short (≤ 2 cm). *Umbels* convex, negatively geotropic, 15–40 flowers. *Flowers*: outer coronal lobes white, acute-acuminate; inner coronal lobes bright red, acute-acuminate; overall lobe shape elliptic; outer coronal lobe tips slightly more elevated than inner lobe tips; corolla faintly pubescent, recurved, ranging from pure white to a pale lemon yellow, usually violet-dotted. *Pollinaria* retinaculum with laterally protruding margins surrounding the cavities where the wingless caudicles are attached.

Distribution — Currently available data suggest that *H. dolichosparte* is endemic to Sulawesi.

Ecology — *Hoya dolichosparte* is a rather common twining vine in central Sulawesi from sea level to approximately 600 m altitude. It was observed growing epiphytically in undergrowth and trees along the sea shore, in large trees along rivers and lakes and in shrubs along plantations. It was also found growing terrestrially on limestone outcrop overlooking the Poso river.

Note — Vegetatively, *H. dolichosparte* bears close semblance with *H. camphorifolia* Warb. Furthermore, growth habit and habitat preference are similar, and the two species are often found growing through one another. In this case only the shape of the peduncle sets the two species clearly apart. The species is undoubtedly a close relative of *H. nicholsoniae* F. Muell.

5. Hoya imbricata Decne. — Fig. 8

Hoya imbricata Decne. in A.DC., Prodr. 8 (1844) 637; Koord., Philipp. J. Sci. 15 (1919) 263, incl. forma *typica*, nom. inval.; DC. in Deless., Icon. Sel. Pl. 5 (1846) 37, t. 90. — Syntypes: *Callèry s.n.* (P n.v.), Philippines, Luzon, 'Calawan' = Manila; Deless., Icon. Sel. Pl. 5 (1846) t. 90.

Conchophyllum maximum H. Karst., Ann. Jard. Bot. Buitenzorg 12 (1895) 158. — *Dischidia maxima* Koord., Meded. Lands Plantentuin 19 (1898) 534. — *Hoya maxima* (H. Karst.) Warb., Feddes Repert. Spec. Nov. Regni Veg. 3 (1907) 342, non Teijsm. & Binn. (1863). — Type: not indicated but obviously Karsten's own collection(s).

Hoya imbricata Decne. forma *basi-subcordata* Koord., Philipp. J. Sci. 15 (1919) 264, t. 2, 3. — Syntypes: *BS 24910 (Edaño)*, Samar, *BS 18893 (McGregor)*, Biliran, *Copeland 399* (all apparently loaned from PNH, now lost), Mindanao, Davao district,

Hoya pseudomaxima Koord., Philipp. J. Sci. 15 (1919) 265. — Type: *BS 22089 (Ramos)* (apparently loaned from PNH, now lost), Philippines, Luzon, Rizal Province, Bosoboso.

Stems thin, sparsely twining, grow out to considerable length before developing a single mature leaf per internode. *Leaves* large, orbicular, peltate, with various degrees

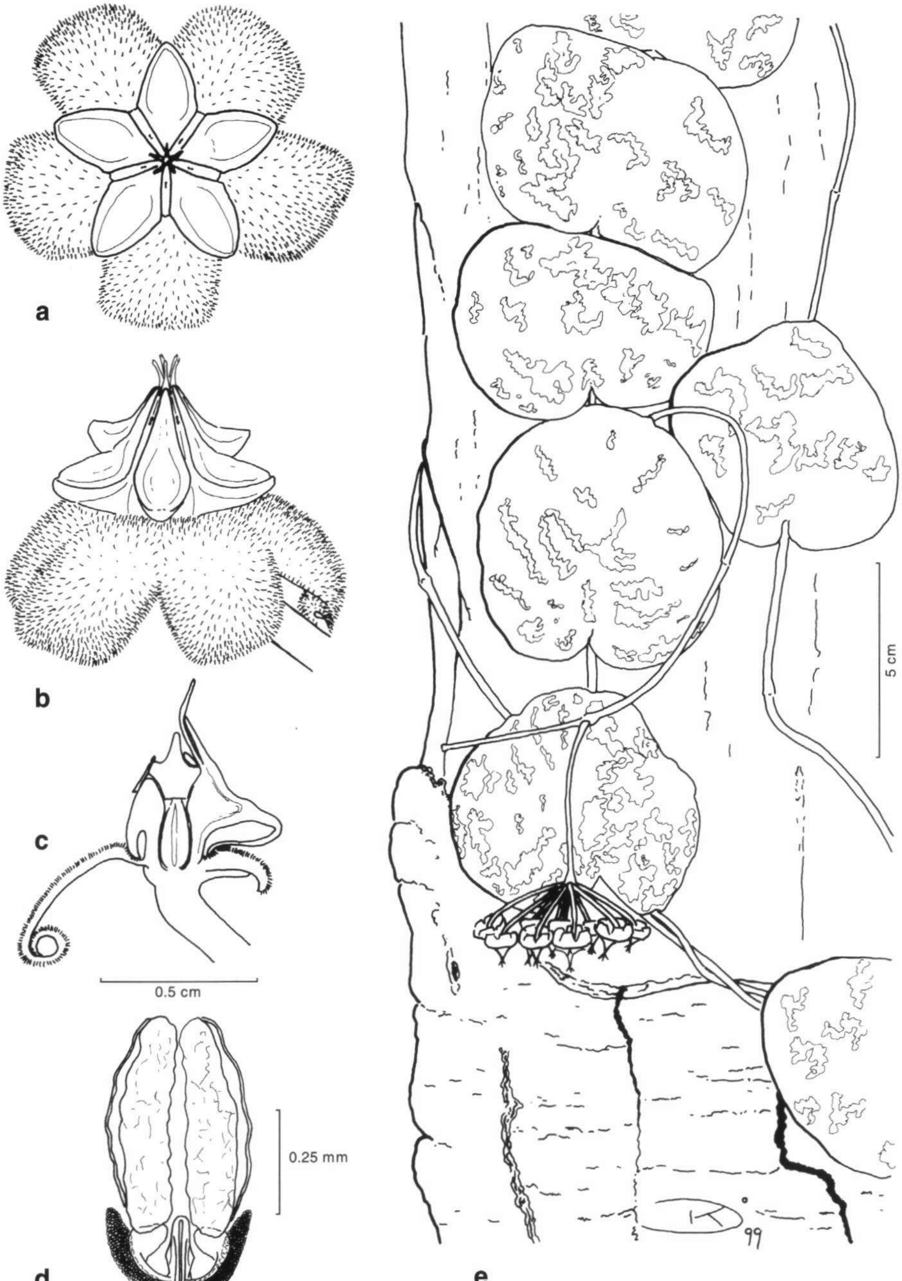

Fig. 8. *Hoya imbricata* Decne. a. Flower in top view; b. flower in side view; c. flower in median section; d. pollinaria; e. growth habit (flowers drawn from live material grown indoors in the Netherlands; *IPPS 8838*. Growth habit drawn from a plant growing on a shade tree in a cacao plantation c. 30 km west of Kolonodale).

of incision of margin towards petiole; covering both stem and adventitious roots, margins pressed tightly against substrate; upper surface with a complex pattern of darker spots superimposed on a lighter background, colour combinations greyish green with brownish purple, green and purplish red or light green and dark green; lower side uniformly dark purple. *Petioles* (sub)peltate. *Peduncles* medium-long to long (> 5 cm). *Umbels* concave, positively geotropic, with 10–20 flowers. *Flowers* white, yellowish white or yellowish white with a shade of red on the inner coronal lobes, inner coronal lobes almost vertical, outer coronal lobes horizontal, anther appendages characteristically long forming a crown on top of the corona, anther wings typically short (Fig. 8b, c), corolla inside densely hirsute, strongly recurved. *Pollinaria* retinaculum narrowly elongated, caudicles with large wings and attached almost at the bottom end of the retinaculum.

Distribution — *Hoya imbricata* was originally reported from N Sulawesi only (Karsten, 1895; Koorders, 1920). Nevertheless, this species is quite common in central Sulawesi from 0 to 600 m altitude and further investigations will probably show that it occurs in the rest of Sulawesi as well. The species also occurs throughout the Philippine archipelago.

Ecology — Just like Koorders' (1920) description of this species in Minahassa, we found it to occur in open rain forests and on the shade trees of abandoned coffee (in our case cacao) plantations (Fig. 8e). In this region it is usually difficult to spot as the pattern, colour and manner of growth (tightly pressed against its substrate) causes it to blend with the tree trunk. Leaves are produced both on stems growing upwards, resulting in leaves with their tips pointing skywards, and downwards with leaf tips towards the earth (Koorders, 1920). *Hoya imbricata* usually grows on the stem of trees, irrespective of the diameter of the stem and, less regularly, on branches. An important factor may be the amount of water and nutrients that passes the rather limited root system as run-off: the more downstream the substrate, the more water will pass. The species rarely grows without ants. These use the space between the imbricate leaves and the stem for housing and collect organic material underneath the leaves. As most roots are also located under the leaves, plant growth is probably enhanced by this activity of the ants. More than one species of ants has been observed to use the leaves of this species for shelter. The flowers scent very sweetly at dusk, but are scentless during the day (Koorders, 1920) indicating nocturnal pollinators.

Notes — Karsten (1895) originally described *Conchophyllum maximum* H. Karst., later *Hoya maxima* (H. Karst.) Warb., after characteristics of two *Dischidia* flowers mistakenly thought to belong to the large imbricate leaves he collected. In the late 19th and early 20th century a number of papers appeared on this truly remarkable species. Probably because the first paper in this series by Karsten (1895) focused on the morphology and physiology of the leaves and stems, these traits played a key role in the separation of two species and a form from the previously described *H. imbricata* Decne. *Hoya maxima* (H. Karst.) Warb., *H. pseudomaxima* Koord. and *H. imbricata* Decne. forma *basi-subcordata* Koord. were distinguished from *H. imbricata* based upon the following characters: 1) presence of stomata on the upper and/or lower side of the leaves; 2) presence of humps on the cuticular cells and/or hairs on the upper side of the leaves; 3) the depth of the incision at the base of the leaves (Koorders, 1919, 1920). Although there is the obvious (minor) variation in flower size and other

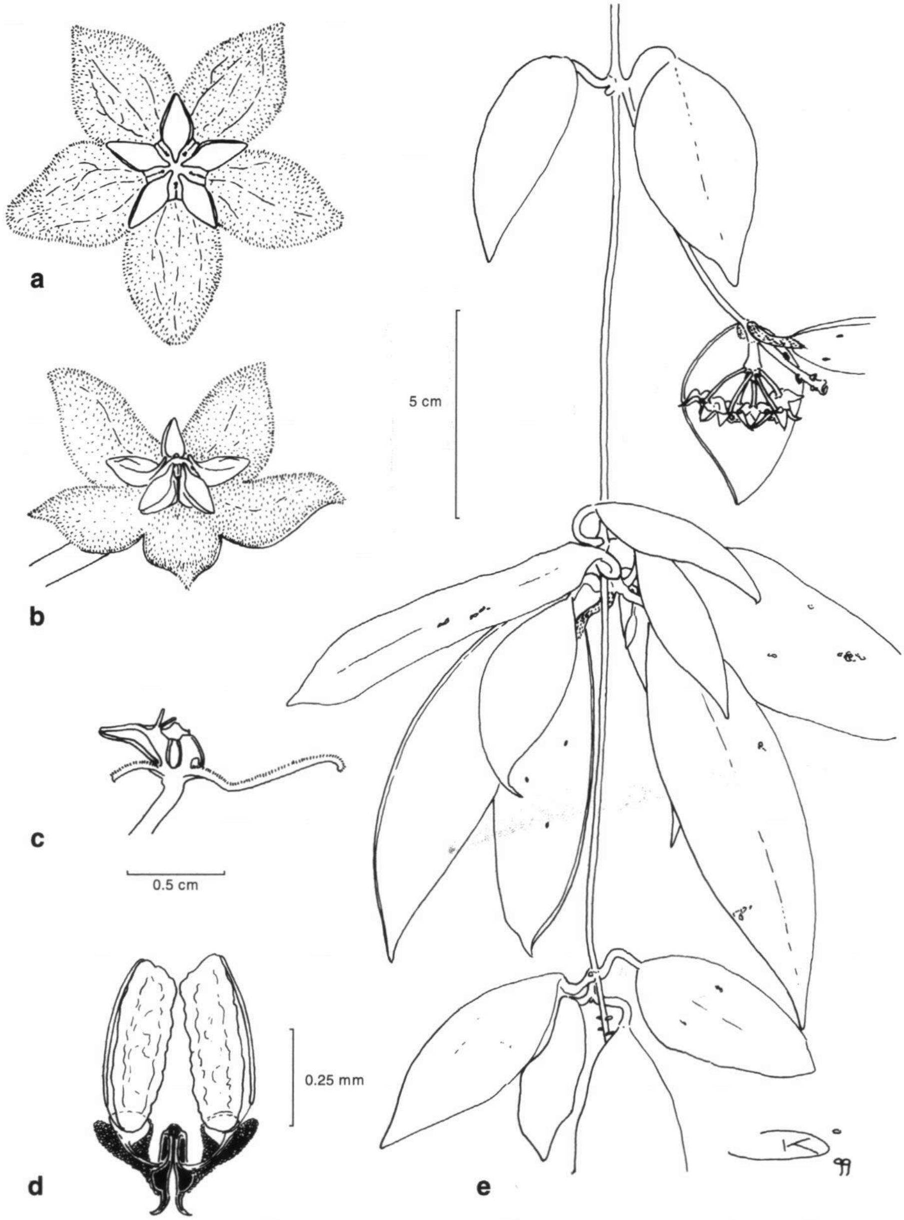

Fig. 9. *Hoya minahassae* Schltr. a. Flower in top view; b. flower in side view; c. flower in median section; d. pollinaria; e. growth habit (drawn from live material grown indoors in the Netherlands; *IPPS 8816*).

floral characters, flower morphology of plants with different types of leaves is relatively constant. We do not think that the variation in above-mentioned vegetative traits justifies the separation of these growth forms into separate taxa. We have therefore placed *H. maxima* (H. Karst.) Warb., *H. pseudomaxima* Koord. and *H. imbricata* Decne. forma *basi-subcordata* Koord. in synonymy with *H. imbricata* Decne. We suspect that *H. shallertiae* Burton was described from a herbarium sheet containing flowers of *H. imbricata* and branches of *Dischidia imbricata*. If so, this species would also be placed in synonymy with *H. imbricata*. The similarities in flower morphology and growth habit (stems and leaves pressed more or less closely against the trunk and main branches of trees) of this species and *H. caudata* Hook. and *H. waymaniae* Kloppenb. suggest close kinship.

6. **Hoya minahassae** Schltr. — Fig. 9

Hoya minahassae Schltr., Beih. Bot. Centralbl. 34, 2 (1916) 15. — Type: *Schlechter 20434* (holo B), Indonesia, N Sulawesi Province, Minahassa, Tomohon.

Stems thick, fleshy. *Leaves* succulent, elliptic, acute to acuminate, venation absent but for a depression where the midrib is. *Petioles* 1–2 cm long. *Peduncles* characteristically short (0.5–1.5 cm), thick. *Umbels* concave, positively geotropic, with 1–6 flowers. *Flowers*: corona and corolla white, overall coronal lobe shape ovate, inner coronal lobes acute, turned upwards almost vertically, outer coronal lobes acute, upper side ridged, corolla densely hirsute, patent to slightly campanulate. *Pollinaria* retinaculum with narrow top and broad, protruding 'hips', retinaculum groove widens significantly downwards from where the caudicles are attached, caudicles with long wings made of honeycomb-structured excretions. [This structure is particularly obvious in this species compared to others; the wings are furthermore uncommon in covering the entire caudicles rather than just the lateral sides.]

Distribution — *Hoya minahassae* is endemic to Sulawesi.

Ecology — Little is known of this species other than that it is confined to mountain areas above 800 m. It was found on the side of the Tineba mountain range (central Sulawesi) facing Lake Poso, which is more humid than the side facing the Bada Valley. Here it grew on moss covered branches of trees in the open mountain forests. It was furthermore found at 1100 m in a mountain range north of Bunku. Schlechter's original specimen was from Tomohon, Minahassa (hence the name) growing at an altitude of some 800 m.

7. **Hoya myrmecopa** Kleijn & Van Donkelaar, *spec. nov.* — Fig. 10

Petioli 0.5–1.5 cm longi. Folia ovata ad elliptica 2.5–7.5 cm longa acuta ad acuminata nervatura obscura. Pedunculi tenues plerumque sursum curvati 1–2 cm longi. Umbellae negative geotropicae convexae floribus minutis 6–16. Corolla coronaque viridiflavide alba; corolla sparse hirsuta sub anthesi valde recurvata corona paulo latiore; coronae lobi exteriores extensionibus bilobatis lobi laterales lateralium integrarum partibus necessariis, apicibus corollam valde superantibus; lobi interiores acuminati apicibus eis apices loborum exteriorum multo superantibus. Caudiculae alis minutis. — Typus: *Kleijn & Van Donkelaar IPPS 8840* (holo L), Indonesia, C Sulawesi Province: c. 10 km west of Tentena on limestone ridge forming the north-western shore of Lake Poso.

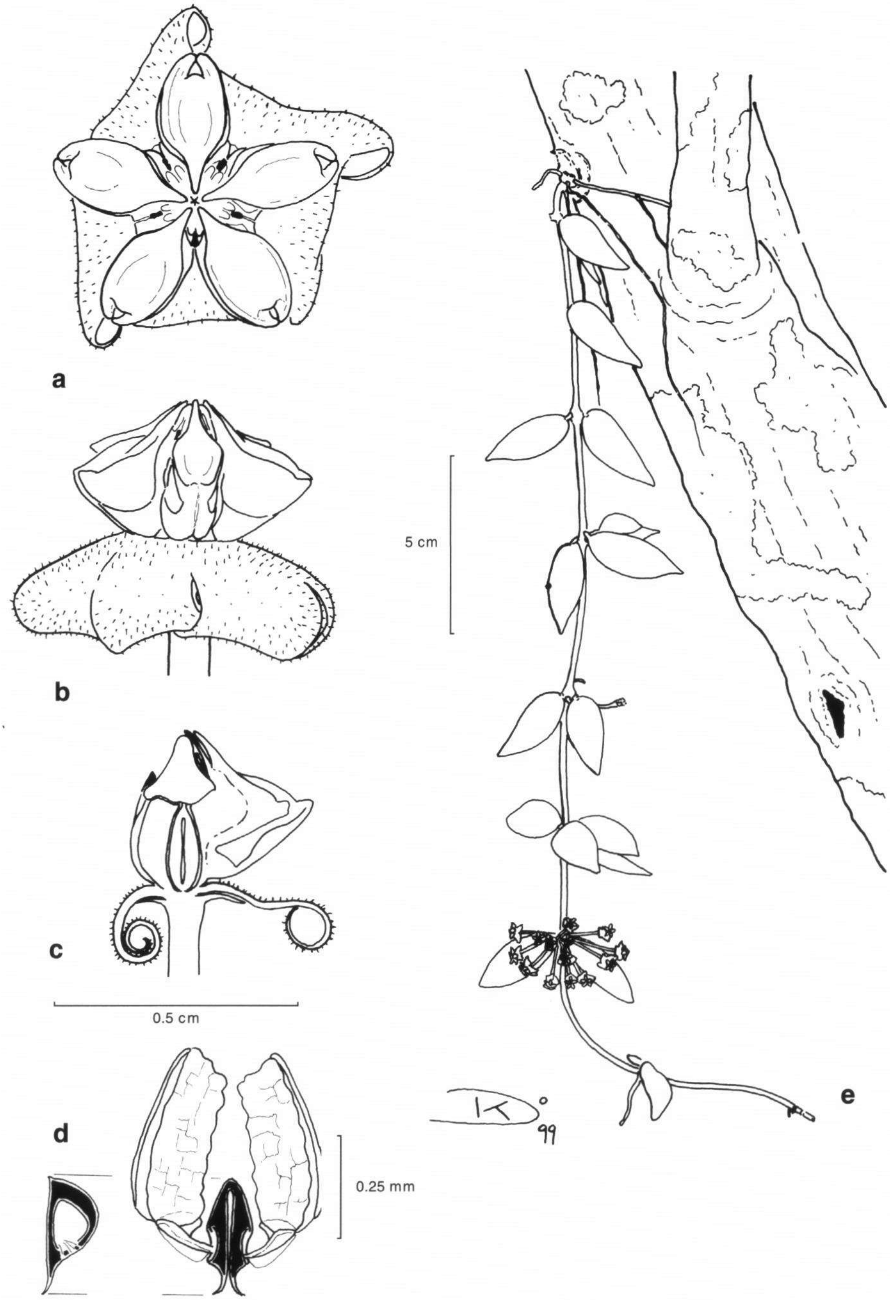

Fig. 10. *Hoya myrmecopa* Kleijn & Van Donkelaar. a. Flower in top view; b. flower in side view; c. flower in median section; d. pollinaria; e. growth habit (flowers drawn from live material grown indoors in the Netherlands, growth habit drawn from the plant growing from the nest of *Tetramorium* ants on limestone ridge on the north-western shore of Lake Poso, which is also the type specimen; *IPPS 8840*).

Leaves 2.5–7.5 cm long, ovate to elliptic, acute to acuminate, venation obscure. *Petioles* 0.5–1.5 cm long. *Peduncles* 1–2 cm long, thin, generally upturned. *Umbels* convex, negatively geotropic, 6–16 small flowers. *Flowers*: corolla sparsely hirsute, strongly recurved, only marginally wider than the coronal lobes, corolla and corona greenish/ yellowish white, inner coronal lobe acuminate, outer coronal lobe with bilobed extensions that are an integral part of the entire lateral sides of the lobe, inner lobe tips much elevated above outer lobe tips, outer lobe tips elevated considerably above corolla. *Pollinaria* caudicles with small wings.

Distribution — *Hoya myrmecopa* was only found in central Sulawesi on the northwestern shore of Lake Poso (± 600 m).

Ecology — *Hoya myrmecopa* is a small leafed, rarely twining species that grows usually as a cluster of stems dangling from the main branches of trees. *Hoya myrmecopa* was found only on the north-west of Lake Poso in the relatively open rain forests on limestone ridges extending from the Tineba mountain range. It was usually found growing from cavities in tree branches. Although in most cavities ant nest material was seen, they were generally abandoned at the time of observation which may have had to do with it being the end of a prolonged dry spell in this area. Once the species was found growing from a small hole in a tree branch (Fig. 10e) which proved to be the entrance to cavities inhabited by ants of the genus *Tetramorium*. Once, it was also observed growing without any sign of ants in the fork of a stem.

Note — The flowers set this species well apart from any other known *Hoya* species in combining characteristics of species from sections within the genus that differ markedly in floral morphology. To our knowledge *H. myrmecopa* is the only species that has both a convex, negatively geotropic umbel and bilobed coronal extensions. However, unlike species from section *Acanthostemma* (Fig. 1, 3, 11), which have extensions that originate from the lower lateral sides of the outer coronal lobe, the extensions of *H. myrmecopa* are an integral part of the entire lateral sides of the lobe. It may represent a phylogenetic link between the sections *Acanthostemma* (e.g. Fig. 3, 11) and *Hoya* (e.g. Fig. 4, 7). The name *myrmecopa* consists of 'myrmex' or 'ant' and 'ope', or 'hole' in Greek, and refers to the niche where this species was commonly found growing.

8. Hoya pallilimba Kleijn & Van Donkelaar, *spec. nov.* — Fig. 11

Caules tenues juniores hirsute, glabrescentes. Petioli 0.5–1 cm longi. Folia ovata 3–8 cm longa acute sine nervatione manifesta, marginibus in dimidio basali pallide viridis. Pedunculi saepe 5 cm longiores hirsuti demum glabrescentes. Umbellae positive geotropicae concavae floribus 15–30. Corolla intus hirsuta valde recurvata; coronae lobi extensionibus bilobatis; exteriores apicibus fere verticaliter sursum erectis; interiores apicibus parum erectis. Caudiculae alis magne alatis, retinaculo in medio sulco latissimo. — Typus: *Kleijn & Van Donkelaar IPPS 8864* (holo L), Indonesia, C Sulawesi Province: Morowali Reserve, near mouth of Ranu River.

Stems thin, hirsute when young, glabrescent. *Leaves* 3–8 cm long, ovate, acute, without obvious venation, margins on basal half of the leaves thin, pale green. *Petioles* 0.5–1 cm. *Peduncles* more than 5 cm long, hirsute to glabrescent. *Umbels* concave, positively geotropic, 15–30 flowers. *Flowers*: corona yellowish, inner coronal lobe points almost vertically upwards, outer coronal lobes have bilobed extensions with tips that point

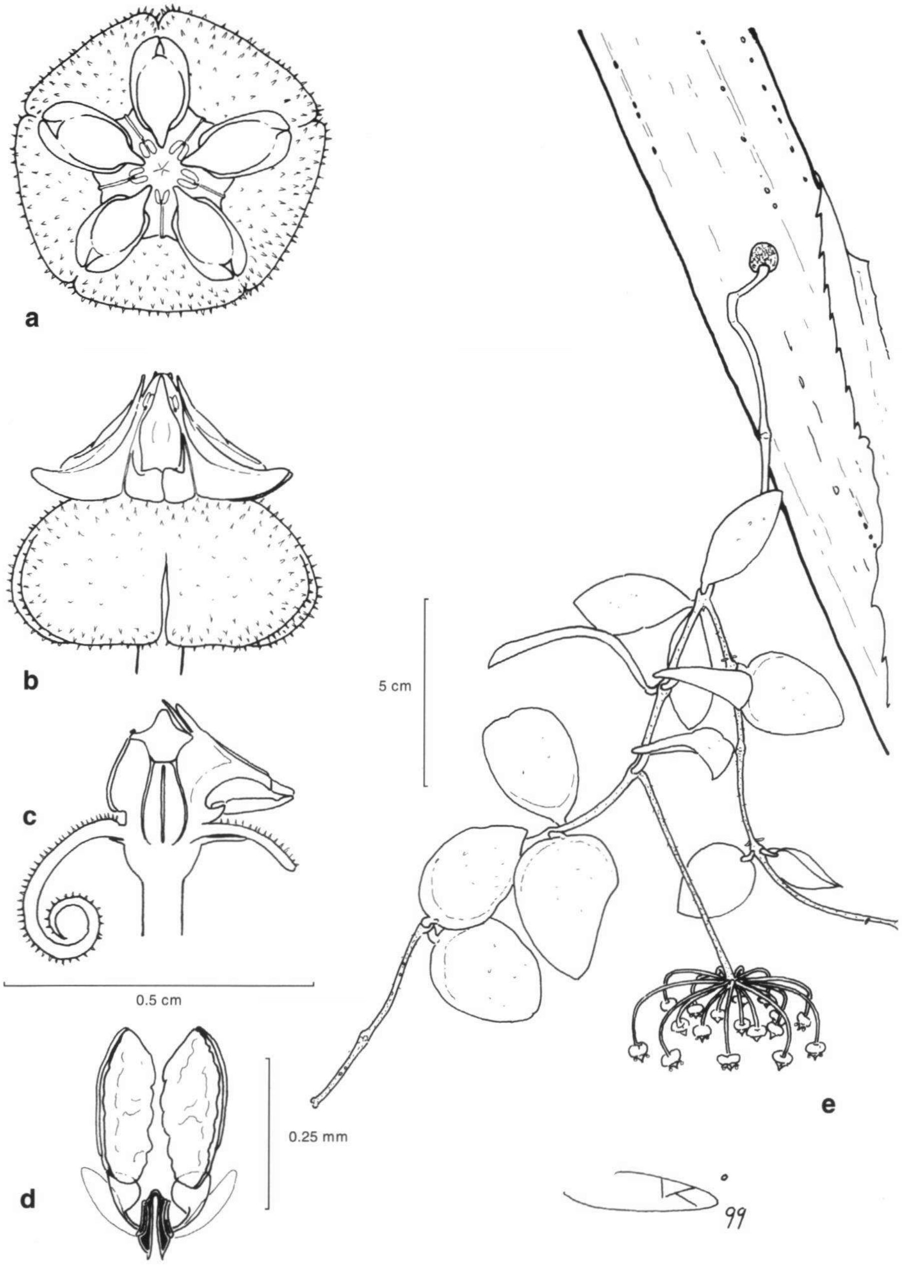

Fig. 11. *Hoya pallilimba* Kleijn & Van Donkelaar. a. Flower in top view; b. flower in side view; c. flower in median section; d. pollinaria; e. growth habit (flowers drawn from live material grown indoors in the Netherlands, growth habit depicts the plant growing from the stilt-root of a *Pandanus* species in the Morowali Reserve, which is the type specimen; *IPPS 8864*).

slightly upwards, corolla dull whitish red, hirsute on the inside, strongly recurved. *Pollinaria* caudicles with large wings, retinaculum with very wide groove in the middle.

Distribution — So far, this species has just been observed on the eastern shores of Sulawesi and nearby on the Tukang Besi Islands.

Ecology — *Hoya pallilimba* probably grows in association with ants. As depicted in Fig. 11e, a plant was found growing from a little circular hole in a stilt-root of a *Pandanus* species. The opening was closed with something resembling ant carton; however, ants were not found when opening the hollow root. The second, and only other observed individual of this species was found growing without any obvious signs of ants on a tree log not far away from the first plant. Both plants grew at sea level on alluvial soils not far from the Ranu River in the Morowali Reserve. As indicated by notes on the herbarium sheets, others have found this species growing on ultrabasic soils (Soroako-Malili Road, *Van Balgooy 3820*, L), on coral-chalk (Tukang-Besi Islands, *Elbert 2537*, L) and in Opa swamp (Polipolia 200–300 m, *Prawiroadmodjo & Soewoko s.n.*, L).

Note — Vegetatively, *Hoya pallilimba* resembles *H. myrmecopa* quite closely. Distinctive is, however, the thin, pale green margin extending downwards from both sides of the petiole until approximately halfway the leaves. From this margin the name of the species is derived: 'palleus' for 'pale' and 'limba' meaning 'margin' in Latin. The thin margin is also distinctive when plant material is dried, e.g. on herbarium sheets.

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IDENTIFICATION LIST

The numbers after the collectors and their collecting numbers refer to:

1 = *H. brevialata*
2 = *H. camphorifolia*
3 = *H. coronaria*
4 = *H. dolichosparte*
5 = *H. imbricata*
6 = *H. minahassae*
7 = *H. myrmecopa*
8 = *H. pallilimba*

Alphonso & Samsuri A.236: 3.
Blume 483: 3; s.n. (L no 898.168-121–125, 898.168-128): 3 — Buwalda 5228: 3.
Chai s.33565: 3 — Chew Wee-Lek CWL 513: 3 — Ching s.38246: 3; 40154: 3 — Church & Ismail 21: 3 — Conklin & Buwaya 80526: 3 — Coode 5984: 3.
De Vogel 5661: 2; 5728: 3; 5793: 4 — De Vriese II: 3; III: 3 — Dransfield 4164: 3.
Edaño 9588: 2; 11015: 5; 34523: 5 — Elbert 3401: 2 — Elmer 15244: 2; 15802: 5 — Eyma 4081: 3; 4192: 3.
Fox 8975: 2 — Frake 36055: 3.
Hallier 247: 3.
Ismail 98903: 3.
Jacobson s.n., Fort A. de Kock: 3 — J.C. 1551: 3 — Jensen 400: 3 — Johansson 105: 2.
Kaudern 173: 5 — Kerr 12447: 3 — Kleijn & Van Donkelaar (all IPPS) 7718: 1; 8816: 6; 8831: 4; 8836: 1; 8838: 5; 8840: 7; 8845: 2; 8864: 8; 8891: 3 — Koorders 16187: 5; 16189: 5; 16192: 5; 16201: 5; 16237: 3; 22126: 3; 26847: 3 — Kornassi 688: 3 — Kostermans 6: 3.
Lam 2659: 3 — Lee s.41868: 3 — Leonardo 3531: 5.
Maingay 1125: 3 — Maxwell 80-39: 3; 85-916: 2 — Meyer 9997: 3.
Posthumus 627: 3.
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Toxopeus 58: 3.
Van Balgooy 4867: 3; 6513A: 3 — Van Niel 3745: 3.
Weir 1: 5 — Whitmore FRI 3707: 3.

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Accepted names are in roman type, new names in **bold** and synonymy in *italic*. Numbers refer to the species numbers as given in the text.