NEW PARASITIC ANTS OF THE GENUS *KYIDRIS*, WITH NOTES ON ECOLOGY AND BEHAVIOR

by

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During the course of a collecting and study tour of New Guinea made by one of us (WILSON) early in 1955, there were discovered on several occasions at different localities remarkable mixed nests, each composed of two widely different species of dacetine ants. The larger of the two different kinds found mixed was always *Strumigenys loriæ* Emery, a common New Guinea species peculiar in its own right because of its frequently highly polymorphic worker caste (SZABÓ, 1910). The smaller of the two nestmates proved to belong in each case to the genus *Kyidris*, a smithistrumiform entity previously known only from Japan and Formosa. Close study has revealed that the New Guinea *Kyidris*, while unmistakably congeneric with the Japanese species, is not of the same species. Furthermore, the aberrant females of the New Guinea samples indicate that at least two different species, both new, are contained in the collection. It is the purpose of this paper to review briefly the present status of *Kyidris*, to describe and name the new species of the genus, and to describe the behavior and ecology of the mixed colonies as observed in the field and in the artificial nest.

THE GENUS *KYIDRIS* BROWN

Kyidris and its monobasic genotype, *K. mutica* Brown (1949) were first described on the basis of a handful of workers collected by H. OKAMOTO on SHIKOKU and sent to Dr. KEIZÔ YASUMATSU, of the University of Kyushu. Dr. YASUMATSU recognized these workers as belonging to a new species of the tribe Dacetini near the genus *Smithistruma* Brown, and sent them to BROWN for description. Comparison with various dacetine genera showed that structurally *K. mutica* is most closely related to the short-mandibulate genera *Serrastruma* Brown (Africa), *Smithistruma* (widespread) and *Weberistruma* Brown (Oriental Region), but that it differs from all of these in the structure of the head and mandibles and, above all, in the high, rounded, bipartite and unarmed alitrunk.

In an addendum to the same paper in which *K. mutica* was first described from the workers (BROWN, 1949), a female belonging to the genus was described as a new species (*K. nuda* Brown) from a single Formosan specimen. This specimen was rather small to fit comfortably as the female caste of *K. mutica*, and it showed reduction of nodal and gastric

sculpture, obsoleteness of the spongiform appendages, modified form of petiolar node and loss of erect hairs as compared to the *K. mutica* workers. Despite these strong differences, unusual for the female-worker separation of dacetines, Mr. OKAMOTO subsequently was able to associate females matching *K. nuda* with workers of *K. mutica* by rearing further Japanese material. Through the cooperation of Dr. YASUMATSU, it was possible to synonymize *K. nuda* under *K. mutica* (Brown, 1952) with a reasonable degree of certainty. It is worth noting that the nests of *K. mutica* were found on Shikoku " ... in the clay soil of somewhat arid place... " and that they were apparently composed entirely, so far as the samples went, of the single species *mutica*. Azuma has found *K. mutica* not uncommon in southeastern Honshu, and we have been able to confirm these records from two workers sent from Azuma's collection. We therefore now know *K. mutica* from central Japan and from Formosa. Though we have no direct reason to consider the biology of this species to be unusual, the fact that the queens are slightly aberrant, and the discovery that the two new Papuasian species described below are parasitic in the nests of *Strumigenys loriae*, lead one to suspect that *K. mutica* may be a temporary social parasite of some species of *Strumigenys* in Japan. By far the most likely candidate as a host is *S. lewisi*, the commonest Japanese species of the genus, and it may be profitable for some Japanese experimenter to try raising *K. mutica* fertile dealates in *S. lewisi* nests. In Formosa, *S. formosensis* Forel is the common *Strumigenys* in most parts. It must be emphasized that a parasitic role for *K. mutica* is at present purely speculative.

The two new species described below from Papua and New Guinea are undoubted members of the genus *Kyidris*. Not only is the *K. media* queen intermediate in size, habitus and sculpture between those of *K. mutica* and the extremely aberrant *K. yaleogyna*, but the workers of all three species are so nearly identical, except in trivial and not very constant characters of size, sculpture and pilosity, that without the accompanying females they might have been assigned to one species. In fact, four stray workers (Accession No. 917) from the lower Busu River, New Guinea, only a few miles from the type locality of *K. media*, are in several ways more like *mutica* than like *media*; without the associated female caste, we cannot say what they are.

As is described in some detail farther below, the Papuasian species definitely show inquilinous behavior and, so far as we know at present, are obligatory in this behavior. Although we have no direct evidence for parasitic nest-founding by the queens, the characteristics shown by this caste indicate strongly that they normally initiate a new colony by entering either a pure colony of the host *Strumigenys* or a mixed colony consisting of *Strumigenys* and their own species, which may thereupon divide by "swarming." If this correspondence really holds, then we might expect to find, following the degree of specialization shown by the females structurally, that *K. yaleogyna* is more specialized in a parasitic direction than is either of its congeners.

A peculiarity of *Kyidris* workers that shows much more strikingly in life than in dead, mounted material is the disproportionate length of the legs, especially noticeable when comparison is made against *Smithistruma* and other close genera. What the function of long legs might be in this case is hard to understand; perhaps one advantage is an enhanced ability to reach higher from the base level, the better to engage in "theft trophallaxis" from host pairs exchanging food (*vide infra*).

THE SPECIES OF *KYIDRIS*

In the descriptions to follow, the abbreviations used for measurements and indices are those of the recent series of studies on the dacetine ants

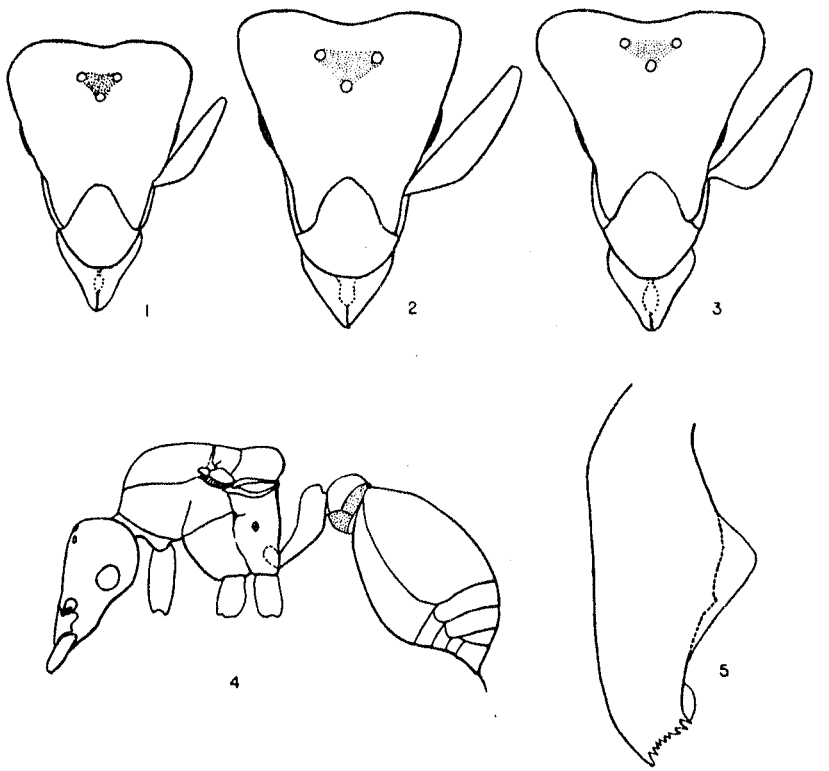

Fig. 1 à 5.

(see especially BROWN, 1949, 1953). The letter "L" used alone or in combination always signifies a maximum measurable length in millimeters. TL is the sum of the axial lengths of the various sections of the body from the tip of the closed mandibles to the gastric apex. HL is the maximum length of the head, including occipital lobes and clypeus, but excluding mandibles. WL is the maximum measurable length, in side view, of the

alitrunk, anterior neck excluded. The letter "I" signifies an index, or percentage relationship of two dimensions. CI, the cephalic index, is the maximum width of the head expressed as a percentage of HL, while MI, or mandibulo-cephalic index, is the length of the exposed portion of the closed mandibles as seen from dorsal view, expressed as a percentage of. HL.

The two new species, *K. yaleogyna* and *K. media*, are based upon females as holotypes, as well as on paratype material of female worker and male castes from the same and other nests from the same localities respectively. All of the Papuasian material was collected by WILSON, and the holotypes from it, together with ample paratype series, will be deposited in the Museum of Comparative Zoology, Harvard University. Other paratypes will be deposited in the Museo Civico di Storia Naturale of Genoa with the Emery Collection, in the United States National Museum, and in one or more public Australian collections.

For *K. mutica*, we have provided an up-to-date synonymy and enough descriptive material to permit a comparison with the new species.

Kyidris mutica Brown.

Kyidris mutica Brown, 1949, Mushi, 20 : 3-6, fig. 1, worker. Type locality: Hirooka, Kamino-mura, Agawa-gun, Tosa Prov., Shikoku, Japan, 30 M. altitude.

Kyidris nuda Brown, 1949, ibid., pp. 23-24, female. Type locality: Mt. Niitaka, Formosa ; synonymy by Brown, 1952, Psyche, 58: 124.

Polyhomoa itoi Azuma, 1950, Hyogo Biology, 1: 35-37, figs., worker. Type locality: Tomogashima, Kii Prov., Japan. Synonymy by Brown and Yasumatsu, 1951, Mushi, 22: 93-95.

Kyidris itoi Creighton, 1950, Psyche, 54: 93-94.

Female : The measurements and indices of the *K. nuda* holotype are taken from the original description: TL 2.21, HL 0.57, WL 0.61 mm.; CI 77, MI 19. Two specimens from the reared Shikoku nest (see under male, below) are even smaller, with HL 0.54-0.55 mm.

Head shape as in fig. 1. Sculpture as in the worker and as in normal *Smithistruma*, etc. females, i. e., reticulate-punctulate over most of head and alitruncal dorsum; however, the sculpture is shallower than usual, in some places feebly shining, and is replaced by smooth, shining areas on the nodes. As in the other *Kyidris* females, the specialized paired erect hairs are absent from the dorsum. The discrepancy in size between this female and its workers is much smaller than that between the respective castes of the Papuasian species, and the sculpture is more nearly normal, but this female still shows a distinct tendency to vary in the direction of the Papuasian forms.

Worker: The type series measured TL 2.00-2.15, HL 0.50-0.54, WL 0.53-0.56 mm., and the indices were CI 76-80 and MI 21-24. A second Shikoku

collection, from the same colony as the males described below and two workers from southeastern Honshu, are about the same in size and proportions. The pairs of large remiform ("oar-shaped") hairs, one pair each on occiput, mesonotum, petiole, postpetiole, anterior gastric dorsum, and several pairs farther back, do seem constant in number and position in this material.

Male: Smaller than the males of the Papuasian species; HL 0.45, forewing L ca. 2.2 mm. Measurement and description from 2 specimens collected by H. Okamoto at Moriyama-mura, Agawagun, Tosa Province, Shikoku, and reared from a nest together with females and workers. Mandibles short, straight, rudimentary, tapering to a simple acute point; it seems that there is no possibility that they can close to meet each other. Postpetiole shining in front, vaguely striolo-punctulate behind; postpetiolar collar reduced to a transverse posterior rudiment, present only in the middle. Genitalia retracted, not examined. Color, except the blackish head, generally lighter, more brownish yellow than in Papuasian species, but it is not certain that this is the full adult pigmentation.

Azuma (*loc. cit.*) found colonies containing up to 1000 workers nesting in "plant cavities", but other notes he gives on these collections are not clear in the translation available.

Kyidris yaleogyna sp. nov.

FEMALE: holotype, alate: TL 3.1, HL 0.70, WL 0.81, forewing L ca. 2.9 mm.; CI 80, MI 16. *Ex* colony no. 610. Paratypes, alate and dealate, TL 3.0-3.2, HL 0.69-0.72, WL 0.81-0.85; CI 79-81, MI 16-17. Two specimens *ex* colonies nos. 610 and 664.

Much larger than its own workers and the queens of *K. mutica*. Head as in fig. 3; the most significant characters of gross outline are the relatively narrow anterior cranium, accompanied by a decided concavity of the converging sides in front of the occipital angles, causing the angles themselves to appear more prominent laterally, and the broadened, anterobasally sublobose antennal scapes.

Mandibles like those of the worker and the new species, *K. media*, shown in fig. 5, but smaller relatively than in the worker and with a reduced number of teeth in the apical series. The size of the individual teeth is reduced toward the middle of the series, and there are only 6 (perhaps a seventh minute tooth is present in some specimens, but the holotype has 6) teeth in addition to the apical tooth proper. Another odd character found in the females of both *yaleogyna* and *media*, but never in the *K. mutica* female or in the workers of any of the three known species, is the low, rounded, transparent lobe situated in the great diastema just proximal to the first tooth of the apical series. In all known *Kyidris* workers, and in the *K. mutica* female, the dentition is alike, consisting of apical plus 11 teeth in the apical series, all rather uniform in size except the first (basalmost) tooth, which is slightly larger (Brown, 1949, fig. Ic).

The alitrunk is even higher and bulkier relatively than in *K. mutica*, and the scutellum projects somewhat to overhang the vertical feebly angled free face of the propodeum. Petiole slightly more massive (deeper) than in *K. mutica*, rounded above and below and with no traces of spongiform appendages. Postpetiole evenly rounded, its spongiform appendages reduced to a heavy, glassy, transparent collar extending around the posterior border and down each side behind, and a fair-sized ventral lobe of the same consistency. Gaster bulky, its dorsal surface smooth, without basal sculpturing of any kind.

Entire body, including most of the appendages, smooth and shining, with a few scattered indistinct punctures on the head, becoming deeper and more elongate on the clypeal surface beneath each of the hairs, and also on the mandibles. In dealate females, however, the integumental surface is normally covered by a continuous sheet of transparent material, apparently a secretion, that renders the surface opaque to subopaque, and sometimes even rough, where it lies.

Ground pilosity very sparse, consisting of small, fine appressed hairs on dorsum of head and alitrunk, mostly directed obliquely mesad; denser and somewhat heavier appressed linear hairs on clypeus, underside of head, mandibles and scapes. Very fine small appressed hairs scattered over gastric dorsum and apex, directed caudad. Erect hairs absent except for a few fine ones at the gastric apex. Color clear light ferruginous, gaster sometimes a trifle darker; appendages more yellowish; ocellar triangle blackened.

WORKER: paratypes: TL 2.2-2.4, HL 0.53-0.59 (0.56), WL 0.55-0.61 mm.; CI 78-82 (80), MI 22-24. Measurements from 14 specimens from 3 different nests. Similar in most respects to the worker of *K. mutica*, but usually slightly larger and a bit darker, with head not quite so thick dorsoventrally, and the node proportionately larger and deeper, though all of these characters show variation in both species. The best distinguishing character appears to be the pilosity. In *yaleogyna*, the appressed ground pilosity is finer on the head and scapes, but coarser and more conspicuous on the nodes and gaster. The paired erect remiform hairs of the occiput, mesonotum and gaster are generally smaller and less conspicuous in *yaleogyna*, and on the occiput especially, they may be missing altogether or else appressed. On the nodes and anterior gastric dorsum, the paired remiform hairs found there in *mutica* are absent or else not clearly differentiated from the surrounding short ground hairs, but even so, *yaleogyna* workers occasionally have one or two of the remiform nodal hairs enlarged, fairly distinct from the rest, and weakly raised.

Basal costulation of gaster interspersed with reticulation, rendering the surface here subopaque to opaque, and extending back to between 1/2 and 2/3 the length of the first gastric segment, or farther than in *mutica*, in which species the costulation rarely extends as far as halfway, and usually ends far short of halfway. The color is a medium to light ferruginous yellow.

MALE: paratypes: TL 2.79, HL 0.54, L head with closed mandibles 0.61, head width including eyes 0.45, without eyes 0.41, WL 0.80, forewing L about 2.75 mm. Measured from a single specimen from colony no. 664; another male from colony no. 647 is slightly larger, HL 0.56 mm.

General habitus as in male of *Smithistruma*; propodeal teeth not developed. Mandibles reduced and slender compared to female and worker of the same species, but curved inward and capable of meeting; apical tooth followed basad by apical series of one to about four teeth, varying with the individual specimen, the teeth followed basad by a variable diastema and a basal lamella more or less like that of the female and worker. Head, alitrunk and appendages densely reticulo-punctulate and opaque, as in *Smithistruma*, and with similar but somewhat effaced sculpture on petiole; postpetiole with dorsal surfaces usually largely smooth and shining, at least in front, its posterior lamelliform collar fairly well developed, projecting as a rim and widened at the sides; no ventral appendages developed.

Pygostyles robust, with long slender hairs. Exserted parameres thick, curving gently mesad, with narrowly rounded apices, their outer (dorsolateral) faces shallowly impressed; mesial borders cultrate, lateral border convex. Volsellae (not removed for flat view) appearing much like those of *Smithistruma lamellignatha* Brown seen in place, i. e., the digitus is straight and slender.

Color blackish-brown, shading to a lighter, usually more yellowish-brown on mandibles, appendages and gastric apex. Forewing with the usual reduced venation of the smaller dacetite genera, only ScR, stigma, basalis, A and r fairly distinct; Rs, M and CuA represented by grooves. Hindwing straplike, with a single short anterior vein in the basal half; hamuli 4, near midlength of wing.

The wings are much alike in all three species and both sexes of *Kyidris* so far seen, except that larger specimens, and especially the females, have the weakest veins slightly better defined than in smaller specimens, in which veins like Rs and M tend to disappear completely. The 4 hamuli are constant in size and position in both sexes of all three species; the units decrease in size apicad.

The holotype (from nest no. 610) and numerous paratypes of all castes were taken from three separate mixed nests with *Strumigenys loriae* (nos. 610, 647, 664) found at Bisianumu, near Sogeri, Papua, at approximately 500 M. altitude in rainforest, March 15-20, 1955 (E. O. WILSON).

Kyidris media sp. nov.

Female: holotype, alate: TL 2.9 (corrected for gastric extension), HL 0.67, WL 0.75, forewing L ca. 2.7 mm. ; CI 82, MI 17. Very similar to *K. yaleogyna* in general habitus and in form of alitrunk, but different in its smaller size; in the shape of the head (fig. 2), which is not so strongly

narrowed anteriorly, and has more nearly straight sides; in the form of the antennal scapes, which are slightly less broad overall and which lack the sublobose broadening of their bases; and in the distinct sculpturing of considerable areas of the body. Mandible as in fig. 5.

Dorsum of head behind clypeus superficially and rather irregularly punctulate-striate in a longitudinal direction, subopaque. Alitrunk indefinitely coriaceous or finely punctulate in large part, weakly shining, the superficially sculptured areas merging into the smoother and more shining discal portions of scutum and pleura. Nodes, gaster and center of occiput for the most part smooth and shining, but the basal half of the first gastric tergum bears very fine, dense, superficial interrupted costulation radiating outward from its basal margin, rendering the surface here subopaque. Legs and antennae very finely punctulate to smooth, generally shining. The postpetiolar appendages are more reduced than those of *yaleogyna* female, consisting in *media* female of only a very narrow semitransparent collar above and a more or less tuberculiform vestige beneath. Pilosity and color similar to those of *yaleogyna* female.

Worker: paratypes: TL 2.2-2.3, HL 0.54-0.57, WL 0.56-0.61 mm.; CI 82-84, MI 23-24. Measurements from two specimens from type nest.

Very similar to the worker of *yaleogyna*, but has the erect paired remiform hairs even more strongly reduced, these being entirely absent from the occiput, nodes and anterior gaster, while the mesonotal and posterior gastric pairs are very small, fine and inconspicuous. However, if the workers from the nearby Busu River locality (no. 917, see below) should prove to belong to this species (*media*), then the pilosity diagnosis would have to be broadened considerably.

Base of gaster above with very fine, sericeous-opaque reticulo-striolation, longitudinally arranged and extending back 2/3 or more of the length of the basal segment, after which the remainder of the gaster is smooth and shining. The usual coarse costulae, still distinct in *mutica* and *yaleogyna*, are reduced to elements so fine in *media* worker that they are merged with the fine reticulate background or intercalary sculpture.

Male: paratype: A single specimen from the type nest series closely resembles the *K. yaleogyna* male, but averages a little smaller, HL 0.51, forewing L ca. 2.4 mm. Posterior lamelliform collar of postpetiole reduced to a very narrow fringing border. Smooth patch on anterodorsal postpetiole restricted in size. The mandibles and exserted genitalia (the latter not dissected) seem to fall within or very close to the range of variation of *yaleogyna*.

The holotype, together with an additional alate female paratype, one male paratype, and six worker paratypes (plus a few additional workers) were taken from a mixed nest (no. 713) with *Strumigenys loriae* at Didiman Creek, near Lae, Australian Mandated Territory of New Guinea, in lowland rainforest, March 29, 1955 (E. O. WILSON).

Kyidris sp.

Four stray workers, sample no. 917, from the lower Busu River, Huon Peninsula, New Guinea, are very small in size: HL 0.45-0.47 (one specimen of the four is headless), WL 0.46-0.48 mm.; CI 77-81. Paired remiform hairs present and well developed on occiput, mesonotum and anterior gastric dorsum, in addition to the posterior gastric pairs. On nodes, pilosity generally much reduced, virtually absent, no large paired remiform hairs. Basigastric costulation dense and reticulated, but ending abruptly before the middle of the first segment.

These are the smallest *Kyidris* workers we have seen from anywhere, smaller even than the Japanese samples. Whether they are merely variant specimens, perhaps nanitics from an incipient nest, of *K. media*, or are representatives of a third Papuasian species, cannot be decided from the present material. It is clear that in this genus, we should be unwise to describe a new species in the absence of the female caste.

ECOLOGY

Kyidris yaleogyna. ACCESSION NO. 610. Bisianumu, Papua; March 17, 1955. Foothills rain forest, relatively undisturbed. The mixed *S. loriae—K. yaleogyna* colony occupied the terminal 18 inches of a large, rotting, moss-covered log lying on the ground at the edge of a small clearing. The wood was "rich-red", at the stage where passalid beetles are typically very prevalent, and except for several central shafts of resistant hardwood, it could be crumbled easily in the hands. The log was removed almost intact to a sheltered place and the colony divided into convenient lots and counted. That this colony is by far the largest recorded for the tribe Dacetini is shown by the following figures, which of course still include only those individuals in the nest at the time it was gathered. *Strumigenys loriae*: 1622 workers, 16 dealate queens. *Kyidris yaleogyna*: 1170 workers, 4 dealate queens, 84 alate queens, 51 males The large number of parasitic workers, almost equaling that of the host workers, is of especial significance and will be commented upon later.

Abundant brood in all stages of development was present, with no obvious numerical predominance of any stage. This filled several dozen well-defined galleries and chambers over an area of a cubic foot or more. Host and parasite pupae (other stages are not readily determinable) were mixed together everywhere; those of the host were somewhat more abundant. The dealate queens of both genera were distributed throughout the brood area. In one chamber a *Strumigenys* and *Kyidris* were found side by side, but the other 18 queens were all taken singly. Nearly every chamber and gallery contained *Strumigenys* and *Kyidris* workers mingling amicably. In some of these cavities the proportions of the two genera

were about equal, but in others there was definite evidence of segregation, i.e. one or the other preponderated almost to the exclusion of the other. This segregation seems to have been at least in part a temporary effect of the different "temperaments" of the two species. When the nest was disturbed, the *Strumigenys* showed a tendency to gather together in cavities back from the broken parts of the log, where they remained quiescent, whereas the *Kyidris* were very restless, wandering steadily from chamber to chamber and only infrequently settling in one spot. The dealate queens showed no particular preference for "segregated" groups of their own species, but were evidently randomly distributed. Not enough pupae were present to determine with certainty whether there was any tendency for species-separation in the brood, but it was WILSON's impression that there was not.

After the nest had been dissected in the field, WILSON established a small section in an artificial nest for further study of behavior and air-mailed another section to BROWN in the United States for independent study.

ACCESSION NO. 664. Bisianumu, Papua; March 18, 1955. This mixed colony was smaller than the one described above. It was nesting in the cavities of part of a spiny *Myrmecodia* pseudobulb lying on the ground. The pseudobulb had obviously fallen from the tree canopy above and had been on the ground for some time. Its undersurface had begun to decay and mingle with the underlying humus, and the portion of branch which had fallen with it had begun to decay; but the bulk of the plant, including its foliage, was still alive. Part of the pseudobulb was inhabited by the *Strumigenys-Kyidris* and part by a small colony of an undescribed species of the ponerine genus *Stictoponera*. The original arboreal inhabitants, probably consisting of a colony of *Iridomyrmex myrmecodiae* Emery, *I. scrutator* Fr. Smith, or *Polyrhachis andromache* Roger, had undoubtedly moved out shortly after the pseudobulb had fallen to the ground, leaving its chambers available for ground-dwelling ants. WILSON has observed spontaneous, emigration of *I. scrutator* out of pseudobulbs within twenty-four hours after they were brought down in the tops of felled trees (Busu River, New Guinea).

The entire dacetine colony was dissected out and the following population count made. *Strumigenys*: workers 243, dealate queens 4. *Kyidris*: 64 workers, 2 dealate queens, 31 males. Adults and brood (pupae) of both species were thoroughly mingled as in the larger colony (no. 610).

ACCESSION NO. 647. Bisianumu, Papua; March 18, 1955. A third mixed colony of *Strumigenys loriae* and *Kyidris yaleogyna* was found in a small rotting log on the ground in a well-shaded portion of the Bisianumu forest. Only a fraction of the colony was collected, and no population count was made.

Kyidris media. ACCESSION NO. 713. Didiman Creek, Lae, New Guinea; March 29, 1955. Margin of lowland rain forest. A small mixed colony was found in a slender rotting log on the ground. The bark of the log was intact and the wood still firm enough so that it could not be broken apart with the hands. Only a fragment of the colony was retrieved. A later count of this sample revealed that the *Strumigenys* workers outnumbered those of *Kyidris* by about three to one. A few alate queens and males of *Kyidris* were present in the nest, but none of *Strumigenys.* Adults and brood of both species appeared to be as thoroughly mingled as in the Bisianumu mixed colonies.

ACCESSION NO. 917. Lower Busu River, near Lae, New Guinea; May 3, 1955. Primary lowland rain forest. Four workers of an undetermined species of *Kyidris* were found foraging under a rotting log lying on the ground. No nest was found.

Food Habits

Studies on feeding behavior in colony no. 610 (mixed *Strumigenys loriae* and *Kyidris yaleogyna)* were made in the field by Wilson and later in the laboratory by Wilson and Brown independently. These ants conformed generally to the behavior already described for other dacetine species (cf. Brown, 1954), but showed two peculiarities of their own which seem to us of considerable significance.

First, strong evidence was obtained that the *Kyidris* workers attend coccids. When the nest of no. 610 was first opened, mealybugs were found clustered on rootlets penetrating the rotting wood of one of the peripheral chambers. These insects were at that time surrounded by a number of *Kyidris* workers. Within a few minutes after the chamber had been opened, two of the workers gently picked up coccids and started to carry them off into a darker part of the nest. When retrieved from the ants, the coccids were found to be living and apparently unharmed Other workers were seen soon thereafter tugging at some of the remaining coccids, but they gave up after a short time and wandered off by themselves. Several others remained motionless in place beside the coccids during the hour or so it took to excavate and explore the entire nest. They thus behaved in marked contrast to their sisters wandering all around them, and gave every impression of behaving as "guards" of the type described by Eidmann (1927) and others in temperate-zone ant genera.

Assuming that our interpretation is correct, this is to our knowledge the first recorded instance of higher dacetines attending honeydew-producing insects. There is a single record (G. E. Bodkin, in Crawley, 1916) of the primitive species *Daceton armigerum* Perty attending scale insects in British Guiana, but the habit seems to have been lost in most of the higher groups of the tribe. Certain Australian dacetines, however, do feed on sugary plant exudates (Brown, 1954).

Another interesting aspect of feeding behavior in the mixed colony was the great latitude of prey choice in comparison with that of other dacetines. At the nest site in the field *Strumigenys* workers were found carrying homeward a small midge and several very small, unidentified worms, probably either nematodes or enchytraeid annelids. In the artificial nest they accepted nearly every small arthropod offered them, including symphylans, diplopods (newly hatched and teneral), thysanurans, and entomobryid collembolans. Other species of *Strumigenys* and *Smithistruma* have been recorded with similarly broad diets (WILSON, 1954), but the general rule in the higher Dacetini, i.e. Orectognathiti, Epopostrumiti and Strumigeniti, is rather rigid specificity for collembolans. It is conceivable that acceptance of prey from among animal groups outside the Collembola was a reason why colony no. 610 was able to attain such extraordinary size.

Both in the field and in the artificial nests, the *Strumigenys loriae* were found to be the principal food gatherers. Hunting behavior in this species follows the pattern described by BROWN and WILSON in previous papers as typical for the genus. On contacting prey, workers open their mandibles to more than 180°, turn quickly to face the prey head-on, and strike quickly and (usually) successfully. In our artificial nests, the workers were very efficient at finding and catching small animals placed within stalking range in the food chamber. Entomobryoid collembolans seemed to be the preferred prey for actual larval feeding.

Compared with the *Strumigenys*, the *Kyidris* workers were almost ineffectual as huntresses. They wandered through the food chambers of the artificial nests like any restless dacetines, but rarely attempted to catch, or succeeded in catching, prey. One was seen to seize a symphylan, pull it backwards, hold it for about thirty seconds without attempting to sting it, and finally release it when it began to struggle. Another seized an entomobryid, pulled it back vigorously, then lost it when the entomobryid kicked with its furcula. Another seized an entomobryid, successfully employed its sting, and was carrying it homeward slowly and awkwardly, when a *Strumigenys* worker came up and took the prey away. Still another *Kydris* was seen carrying an entomobryid at a brisk clip across the food chamber floor; it actually reached the entrance to the brood chamber before a *Strumigenys* met it and took its prey away.

The general impression was gained that predatory behavior has degenerated, but not completely disappeared, in the *Kyidris*. In the artificial nests, at least, the *Strumigenys* did the large part of the productive hunting. At the same time it must be recalled that at the nest site, only the *Kyidris* seemed to be associated with the coccids, although of course whether honeydew played any significant role in the colony's economy is completely unknown.

Brood Care and Adult Trophallaxis

Both species were solicitous toward the brood in colony no. 610, as shown by the readiness of both to move it when the brood chamber was exposed to light. There was no apparent prejudice on the part of either species for its own brood; each carried brood of either genus indiscriminantly and with equal care. As in the case of food gathering, however, the *Strumigenys* played the dominant role, and action on the part of the *Kyidris* tended to be infrequent and ineffectual. Both species were observed licking the brood. In one colony fragment containing brood of the *Strumigenys* only, the three *Kyidris* workers present spent much of their time licking the *Strumigenys* eggs, but despite close watching, we never saw a *Kyidris* do damage to an egg.

Adult trophallaxis was observed in the following combinations between the two species: *Strumigenys* donating to *Strumigenys*, *Strumigenys* donating to *Kyidris*, and *Kyidris* donating to *Kyidris*. It is possibly significant that there was no case recorded of the presumed parasite (*Kyidris*) donating to the host (*Strumigenys*). Moreover, in one instance recorded, a *Kyidris* worker interposed itself between two *Strumigenys* workers engaged in trophallaxis and began glossating the donor's mouthparts, whereupon the *Strumigenys* acceptor withdrew. On another occasion, a *Kyidris* worker diverted to itself for several minutes part of the ingluvium being passed from a *Strumigenys* worker to a *Strumigenys* dealate queen. This particular action, which might be termed "trophallactic theft", plus the fact that no *Kyidris* were seen donating to *Strumigenys* in trophallactic exchange, appear to us to be manifestations of a parasitic relationship, but not enough observations of this sort were made to settle the matter conclusively

Nest Building.

Soon after capture, a large section of colony no. 610 was placed in a a bottle with a quantity of nest material and the nest building activities subsequently watched. The *Strumigenys* workers were very active in this work, excavating incessantly over a period of several days, and piling heaps of loose wood and soil around multiple entrance holes. The *Kyidris* workers, on the other hand, were never observed to be engaged in nest building, but spent all of their time wandering restlessly through the galleries of the nest and over the nest surface.

Parabiosis or Primitive Social Parasitism ?

The relationship between *Strumigenys loriae* and the New Guinea *Kyidris* is of a kind which to our knowledge has never before been recorded in ants. In several ways it resembles parabiosis, as described by Forel

and other authorities in certain South American ants (cf. Wheeler, 1921). In these cases, two species belonging to different genera live in the same nest and use the same principal foraging trails. However, food gathering is carried on independently and the broods are kept strictly segregated. There occurs no contact between the two species that could be termed "social" in the strict sense. No interspecific trophallaxis is known to occur and most of the species have been found living independently as well as parabiotically.

The *Strumigenys-Kyidris* mixed colonies of New Guinea resemble the compound colonies of the South American parabionts in that they occupy the same nest. Moreover, food gathering is probably conducted in a more or less independent fashion, since each worker hunts by itself. But the *Strumigenys* and *Kyidris* go much further in the intimacy of their relationship. The brood of the two species is completely mixed, and is cared for, apparently without discrimination, by both species. Furthermore, there is free interspecific adult oral trophallaxis, at least from *Strumigenys*, as the donor, to *Kyidris* as the acceptor.

There is evidence that the *Kyidris* species are not independent of the *Strumigenys loriae*, as in the case of the parabionts, but that they actually live as obligatory parasites. This evidence can be summarized as follows.

1. No independent colonies of *Kyidris* were found in Papuasia. The four colonies of this genus discovered there were in each case mixed with *Strumigenys loriae*. On the other hand, independent colonies of *Strumigenys loriae* are abundant at the same localities and elsewhere.

2. The *Kyidris* workers, as compared with those of the associated *Strumigenys*, were almost ineffectual in hunting prey ; they were less active in moving brood when the nest was disturbed; and they did not participate at all in nest-building.

3. The intrusive method of solicitation practiced by the *Kyidris* on trophallactic pairs of *Strumigenys* is unusual among dacetines, and if it is a frequent occurrence, it would seem to indicate parasitic tendencies. Moreover, no instance of food donation by *Kyidris* to *Strumigenys* was observed, but as already noted, observations of trophallactic pairs were generally too few to make a point of this negative evidence.

4. The queens of *Kyidris yaleogyna*, and to a lesser extent those of *K. media* and *K. mutica*, show several modifications generally associated with parasitic habits in ants; these include a loss of pilosity, a smoothing of body sculpturing, a reduction in mandibular dentition, and possibly also the transparent film sometimes found on dealates.

5. Only *Kyidris* winged reproductives were present in the mixed colonies. This is, however, of limited significance, since winged reproductives were found in only a fraction of the "uninfested" *Strumigenys* nests during the same period.

6. Worker polymorphism of *Strumigenys loriae* was greatly reduced in the mixed colonies, the soldier caste being few in numbers or absent.

7. Limited introduction experiments carried on by BROWN seemed to

show that *Kyidris yaleogyna* workers are much more conciliatory when introduced into strange *Strumigenys* nests than are workers of the non-parasitic dacetines *Strumigenys loriae* and *Smithistruma nigrescens.* Workers of the latter two species, when encountering workers of a strange species (such as *Strumigenys nidifex* of the Fijis) show immediate hostile behavior. A *Kyidris yaleogyna* worker introduced into a *nidifex* nest, on the other hand, made what appeared to be "supplicatory" motions, raising its head and antennae and lifting and moving its forelegs in a "pawing" movement. It made no aggressive moves on its own part, but was threatened and finally killed by the *nidifex* workers.

In our opinion the New Guinea *Kyidris* represent a very primitive level in the development of permanent, non-dulotic parasitism of the sort in which the host queen is preserved and the mixed colony can persist as such for an indefinite period of time. We would like to re-emphasize those features which we consider to be primitive in this respect: the parasite worker caste has undergone very little if any morphological change certainly identifiable with a parasitic mode of life; the parasite worker population is extraordinarily large in proportion to the host worker population; the parasite workers contribute something to the labor of the colony by hunting and brood-handling, although they show little efficiency in these tasks. We have no information as to how the parasitic queens found their colonies, but as mentioned previously, the morphology of the queens suggests intrusion into host colonies by means of conciliatory behavior. Moreover, the increment of both parasite and host queens in the mixed colonies may indicate that the *Strumigenys loriae* tend to be generally amicable toward alien queens of both the parasite and their own species.

Summary.

Two new species of the dacetine ant genus *Kyidris* from New Guinea are described. These were always found in mixed colonies with the larger, polymorphic dacetine species *Strumigenys loriae* Emery, which often occurs independently and is generally abundant in the lowland rain forests of New Guinea. The relationship of the *Kyidris* to the *Strumigenys* is interpreted as a very primitive level of permanent, obligatory, non-dulotic parasitism. Multiple queens of both genera occur together, and the brood is completely mixed. The worker population of the parasite is very large, and in one colony studied almost equaled that of the host. The parasite workers contribute to the colony labor by food-gathering and brood-handling, but are relatively inefficient in these tasks; they apparently do not participate in nest building at all.

Résumé.

Cet article décrit deux espèces nouvelles de *Kyidris* de la Nouvelle Guinée, genre de fourmis dacétines. Elles ont été trouvées toujours en colonies mixtes avec *Strumigenys loriae* Emery, grande dacétine polymorphe vivant souvent sans son parasite et commune partout dans les forêts humides tropicales à basse altitude de la Nouvelle Guinée. Les relations entre *Kyidris* et *Strumigenys* sont interprétées comme un stade primitif de parasitisme permanent, obligatoire et non-dulotique. De nombreuses reines des deux genres se trouvent ensemble dans le même nid, et leur couvain est complètement mélangé. Les ouvrières du parasite sont très nombreuses et, dans une des colonies étudiées, étaient presque aussi nombreuses que celles de l'hôte. Les ouvrières contribuent au travail de la colonie en recueillant de la nourriture et en soignant le couvain, mais d'une façon relativement inefficace; elles ne paraissent pas participer à la construction du nid.

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Figs. 1-5. — Females of the genus *Kyidris*. 1, *K. mutica* Brown, full-face view of head, Moriyama-mura, Tosa Prov., Shikoku, Japan. 2, *K. media sp. nov.*, full-face view of head, paratype. 3, *K. yaleogyna sp. nov.*, full-face view of head, paratype *ex* type nest. 4, Same, lateral view of body. 5, *K. media, sp. nov.*, right mandible of paratype. (Figs. 1-3 drawn to the same scale.)