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TAXONOMIC STUDY ON GALL APHIDS, COLOPHA, PARACOLOPHA AND KALTENBACHIELLA (APHIDOIDEA : PEMPHIGIDAE) IN EAST ASIA, WITH SPECIAL REFERENCE TO THEIR ORIGINS AND DISTRIBUTIONAL PATTERNS

By SHIN-ICHI AKIMOTO

Abstract

AKIMOTO, S. 1985. Taxonomic study on gall aphids, *Colopha, Paracolopha* and *Kaltenbachiella* (Aphidoidea: Pemphigidae) in East Asia, with special reference to their origins and distributional patterns. *Ins. matsum. n. s.* 31 : 1-79, 27 tabs., 32 figs. (28 text-figs., 4 pls.).

Eight East Asian species of the tribe Tetraneurini (exclusive of *Tetraneura*) are revised with remarks on their biology and distribution. *Colopha moriokaensis* (Monzen, 1923), a common gall aphid occurring on *Zelkova serrata*, is synonymized with *Paracolopha morrisoni* (Baker, 1919) known from North America, and *Paracolopha takahashii* sp. nov. is described from Japan. Based on this treatment the Tetraneurini are to include *Paracolopha* in addition to *Colopha, Kaltenbachiella* and *Tetraneura*. *Colopha graminis* (Takahashi, 1930) is synonymized with *C. kansugei* (Uye, 1924), which is shown to have a wide range from East Asia to Nepal. *Kaltenbachiella spinosa* sp. nov. is distinguished from *K. japonica* based on its radically altered life mode from the latter. Poorly known species, *K. nirecola* and *K. elsholtriae*, are redescribed in detail, but the life cycle of the latter is yet unknown. *K. glabra* sp. nov. is described from *Ulmus uyematsui* occurring in the mountain region of Taiwan. Based on the distributional pattern and on paleobotanical information of the host, the original time of each genus is discussed. Whether a genus passed through the Beringian region or not is emphasized as a critical criterion for the original time. *Colopha* has disjunctive ranges isolated in East Asia, central Europe and eastern North America. From this pattern it is considered that *Colopha* originated before the middle Miocene and has maintained diagnostic characters as genus over 10 and some million years in each region. *Kaltenbachiella* and *Tetraneura* are associated with the most prevailing section of *Ulmus* whose distribution is continuous and extensive. In terms of the history of the host plants *Kaltenbachiella* is postulated to have passed through the Bering Land Bridge in later times than *Colopha. Tetraneura* is of Eurasian origin and may have originated from the late Miocene to the Quaternary. The natural range of *Paracolopha* is yet problematical, and alternative possibilities are proposed. The distributional patterns of the Tetraneurini show that the tempo of evolution differs crucially among the 4 genera and that the concept of evolutionary stasis is the most probable explanation for this situation.

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INTRODUCTION

The Tetraneurini are a group of aphids forming globular, bug-shaped, or cockscomb-shaped closed galls on the primary hosts, *Ulmus* and *Zelkova*. They belong to the Eriosomatinae (sensu Heie, 1980), while the other aphids of the subfamily, when occurring on these plant genera, make various open galls. Most of the Tetraneurini seasonally alternate their host plants. From early to mid summer the alates migrate from ripe and opened galls to the secondary host, various herbaceous plants, where the exules pass through some generations during summer. In autumn there appears on the secondary host plants a generation of alates, which remigrate to the primary host and produce the sexual generation. Generations occurring on the primary host and those on the secondary host are so different morphologically as to look as if they belong to different taxa. This has often caused taxonomic confusion resulting in frequent synonymy and wrong species concepts based on erroneous combinations. In East Asia such confusion still remains. Further, the presence of permanent parthenogenetic populations aggravates the difficulty. In many species populations maintained by parthenogenesis on the secondary host plants are distributed beyond the ranges of the primary host plants. There are even species which have been maintained only by parthenogenetic generations after the loss of the holocyclic mode of life. Such species are often problematical as to their taxonomic positions. Integrated recognition of the different morphs is, therefore, indispensable for erecting a sound classification. In the present study much attention has been paid to the first instar larvae borne by the emigrants, because it appears that they often afford clues as to the connection between morphs.

The Tetraneurini (Byrsocryptini sensu Börner and Heinze) have generally been recognized as containing three genera, *Colopha, Kaltenbachiella* and *Tetraneura* (Börner and Heinze, 1957 ; Zwölfer, 1957 ; Heie, 1980). In the course of this study it has been found that another genus, *Paracolopha* Hille Ris Lambers, 1966, is referable to the tribe. This genus has been represented by one species originally recorded on the secondary host in North America. In Japan a well-known aphid making petiolate-globular galls on *Zelkova* has been referred to *Colopha, Tetraneura*, or *Dryopeia* by authors. In the present study this holocyclic Asian form has proved to be conspecific with the anholocyclic American one. The primary host and diagnostic characters of the exule make the exclusion of the species from the genus *Colopha* quite reasonable. Further, another species which was collected on the secondary host in Japan is referred to *Paracolopha*.

The type-specimens of the species which were described from Japan have been lost. I establish neotypes for the species in this paper. Every specimen examined is given the same number on the slide as in measurement and specimen data. All specimens used, including the holotypes and neotypes designated, are deposited in the collection of the Entomological Institute, Faculty of Agriculture, Hokkaidô University.

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DIFFERENCES IN GALL FORMATION BETWEEN COLOPHA-GROUP AND KALTENBACHIELLA

Colopha and *Paracolopha*, hereafter called the *Colopha*-group, and *Kaltenbachiella* are most clearly distinguishable by their gall positions within a leaf, as already pointed out by Börner and Heinze (1957). In the *Colopha*-group the gall is formed on an intercostal region and in *Kaltenbachiella* just on the midrib and usually on the base. The difference in the gall positions seems to result from the behavioural difference in the gall makers, that is the fundatrix first instar larvae, between the two groups. I observed the gall-forming behaviour of fundatrix larvae of *Paracolopha morrisoni* and *Kaltenbachiella japonica* as representatives of the two groups at Sapporo, North Japan in 1981 to 1984. At Sapporo the fundatrix larvae of both species hatch from overwintered eggs from early to mid May, when buds of the host *Ulmus davidiana* var. *japonica* are rapidly developing leaves. The fundatrix first instar larva of *Paracolopha morrisoni* settles on the underside of a just developing leaf which is folded along the midrib at an angle of about 90 degrees, and stimulates the leaf chemically by inserting the stylet at an intercostal site. This stimulus brings on a shallow hollow in a few days (Plate IIA). In this stage the larva is exposed and easily visible from the outside. The hollow grows deeper and larger, involving the settling fundatrix, and then is completely closed. The projection thus formed on the dorsal side of the leaf further develops upwards finally to a petiolate-globular gall.

The fundatrix larva of *Kaltenbachiella japonica* always settles on the underside of young leaf, closely along the lateral side of the midrib as if it conceals itself behind the midrib. Chemical stimuli given by the stylet on the border of the midrib and mesophyll form a narrow groove along the border. The groove takes the fundatrix into the inside, and is soon closed. Thus, the fundatrix larva resides in a cell placed on the lateral side of the midrib. In the first stage of gall development the midrib swells laterally and downwards in proximity to the resident site (Plate IIIA). Subsequently, a spinous globular projection begins to grow upwards on the dorsal side of the midrib (Plate IIIB).

The process of gall development is more gradual in *K. japonica* than in *P. morrisoni*. In the Hokkaidô University campus, when *K. japonica* galls are still growing (Plate IIIB), *P. morrisoni* galls have been completed (Plate IIB and C) in

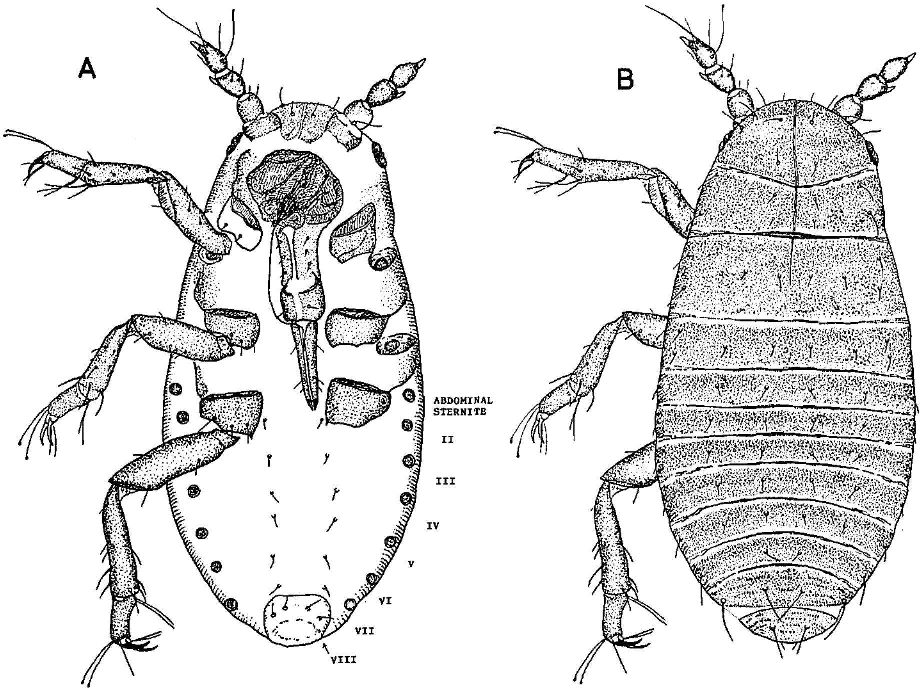

Fig. 1. *Paracolopha morrisoni* (Baker, 1919), fundatrix first instar larva. A Ventrum, B Dorsum.

spite of the fact that both species hatch almost simultaneously. The delay also affects the emerging time of the alates: *P. morrisoni* emigrants appear in early July, while *K. japonica* emigrants in late July to early August.

The fundatrix larvae of the two species conspicuously differ in morphology (Figs. 1 and 2), and this may result from the difference in the manner of gall formation. The first instar larva of *P. morrisoni* is wholly and evenly sclerotized on the dorsum. This characteristic may be adaptive in connection with its exposed conditions at the incipient stage of gall formation. The larva of *K. japonica* has only weakly sclerotized fragmentary plates mainly on the thoracic terga. It is obviously smaller (about 80% as large as *P. morrisoni* in body length), although the two species do not so much differ in the body size of the sexuparae (about 85%), which should determine the size of the sexuales and, then, also of the fundatrix larvae (Tables 3 and 5). Further, *Aphidounguis mali* almost agrees with *K. japonica* in the size of sexuparae (about 89% as large as the latter in body length), but is much superior to it in the size of fundatrix larvae (about 141%, Table 1). These facts suggest a direct effect of selection exerted on the size of the fundatrix larva of *K. japonica*. This suggestion is supported by the fundatrix adult of *K. japonica*, which is, to the contrary, superior to that of *P. morrisoni* in body size on the average (Tables 22 and 23).

The assumption that a species forming the gall under exposed conditions tends to be large in size and sclerotized on the skin is corroborated by the genus *Tetraneura*. All the species examined of the genus are larger in body size and more

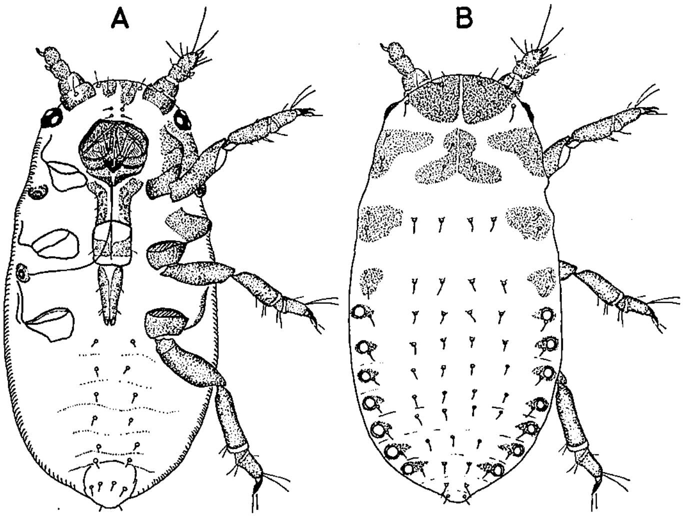

Fig. 2. *Kaltenbachiella japonica* (Matsumura, 1917), fundatrix first instar larva. A Ventrum, B Dorsum.

intensively sclerotized than *P. morrisoni* (Table 1). Patch's (1910) description also shows that the fundatrix first instar larvae of the genus *Colopha* have wholly or nearly wholly sclerotized dorsum: "Smooth, dark olive-brown in color with black members. After first molt, ···· the color is paler, but the members are still black."

Consequently, the fundatrix first instar larva of *Colopha*-group is characterized by wholly, evenly sclerotized dorsum. That of *Kaltenbachiella* must have been selected to become small and delicate because of a lengthened stay in a narrow cell within the midrib. The concepts of *Colopha* and *Kaltenbachiella* often become ambiguous if only exule generations are took into account (Stroyan, 1964), but fundatrix first instar larvae as well as galls successfully distinguish the two genera.

GENUS PARACOLOPHA HILLE RIS LAMBERS, 1966

Diagnosis. Exule adult—Body almost elliptical. Head and prothorax rather extended long from broadly rounded abdomen. Antennae 5-segmented or with an incomplete slit on segment III, 0.10-0.15 times as long as body; segment IV broad; segment V narrower and longer than IV. Legs short. Tarsus 1-segmented or completely separated to 2 segments, not strongly tapering. First segment of fore tarsus thickened and projecting anteriorly. Rostrum long, 0.3-0.4 times the whole length of body; ultimate segment slender, converging with almost straight margins. Wax gland plates arranged longitudinally in 6 rows but reduced to 4 rows in abdominal tergites V-VII and 2 in tergite VIII, almost oval-shaped or strongly extended transversely, consisting of central field(s) and circular or oval circumferential cells; the central field of *P. morrisoni* separated into some irregular spaces. Cornicles always present on abdominal tergite V, rather projecting, surrounded thinly by setae, without pore, not sclerotized around. Body setae short, thinly distributed. Genital plate not pigmented, posteriorly curved, with transverse rows of minute denticles, with setae along hind margin; without a pair of long setae in the central part. Anal plate forming 2 indistinct lobes. Sclerotized plate present or absent on each side of genital plate.

Composition. This genus at present includes two species, *Paracolopha morrisoni* and *P. takahashii*. As mentioned later, *P. morrisoni* is likely to be of East Asian origin and associated with *Zelkova serrata* and small bamboos, respectively as the primary and the secondary host. *P. takahashii* was collected on the basal part of *Carex* in Japan.

Paracolopha morrisoni (Baker, 1919)

Dryopeia morrisoni Baker, 1919 〔originally described from North America〕.
Tetraneura moriokaensis Monzen, 1923 〔recorded from Japan〕. Syn. nov.
Watabura moriokensis : Monzen, 1929, p. 29-31 〔redescribed, illustrated, with biological note〕.
Watabura nishiyae : Matsumura, 1931, p. 1298 〔illustrated with biological note〕.
Tetraneura nishiyae : Takahashi, 1931, p. 102 〔short comment for synonymy〕.
Tetraneura moriokaensis : Mordvilko, 1935, p. 131 〔redescribed with record on small bamboo in Taiwan〕.
Dryopeia nishiyae : Shinji, 1941, p. 1070-1072 〔illustrated with remarks〕.
Byrsocrypta moriokaensis : Börner and Heinze, 1957, p. 292.
Dryopeia nishiyae : Tanaka, 1961, p. 28 〔with photograph and short comment〕.
Paracolopha morrisoni : Hille Ris Lambers, 1966, p. 600-601 〔original description of genus〕.
Colopha moriokaensis : Hille Ris Lambers, 1967, p. 88-89 〔comment for taxonomic position〕.
Colopha moriokaensis : Higuchi and Miyazaki, 1969, p. 55 〔host plant〕.
Colopha moriokaensis : Eastop and Hille Ris Lambers, 1976, p. 160.
Colopha moriokaensis : Sorin, 1977, p. 9 〔short comment on biology〕.
Colopha moriokaensis : Sunose, 1980 〔predation by birds〕.
Tetraneura zelkovisucta Zhang, 1980 〔record from southern China〕. Syn. nov.
Colopha moriokaensis : Moritsu, 1983, p. 214 and p. 455 〔photograph and illustration〕.
Tetraneura zelkovisucta : Zhang and Zhong, 1983, p. 86-87.

Remarks. The aphid, which forms pouch galls on *Zelkova serrata* and has *Sasa* spp. as the secondary host, is one of the most common gall-makers in Japan. The species was described under the name *Tetraneura moriokaensis* in Japan by Monzen (1923), and has been referred to some other genera. Hille Ris Lambers (1967) already noticed that the Japanese aphid is possibly conspecific with the American *Paracolopha morrisoni* owing to a close similarity in the embryos. Nevertheless, he transferred the former to *Colopha*, because the adult exule of *P. morrisoni* is characterized by having large cornicles subspinally, while the Japanese aphid was described by Monzen (1923) as having no cornicles. However, in the present study it has been found that the Japanese aphid has well-developed cornicles and cannot be distinguished from the American species. The Japanese form well agrees with the latter also in the sexupara in the characters of the antennae, secondary rhinaria, cornicles and wings so far as compared with the description and illustration of the alate form of the American species prepared by Baker (1919) (Table 3). *Tetraneura moriokaensis* should be united with *Paracolopha morrisoni* in one and the same species.

Paracolopha morrisoni was recorded three times in North America : first, on 21 March, 1916, on the roots of potted *Phyllostachys* in Maryland (Baker, 1919), and further, on bamboo-roots in a nursery in southern California and on the roots of *Arundinaria gigantea* (= *macrosperma*) in South Carolina (Hille Ris Lambers, 1966).

These records except the last were made under artificial conditions. *Phyllostachys*, generally large-sized bamoos, is not native to North America and probably has been introduced from Japan. Moreover, southern California is one of the areas where many bamboos were imported from East Asia. Therefore, it may be supposed that *P. morrisoni* found in North America was originally transferred from East Asia by artificial means.

The record on *Arundinaria macrosperma*, a plant native to southeastern United States, may simply show that the parthenogenetic form spread widely from imported plants and acquired native plants as its hosts. In Japan, however, *Phyllostachys* bamboos have not been recorded as secondary hosts of *P. morrisoni* although they are known to be infested by *Prociphilus take* (Shinji, 1941). From Baker's remarks it is certain that in Maryland apterous individuals hibernate on bamboo-roots and begin to reproduce in March and that the next generation grows to the alate form. Such biology has not been known in the Japanese form. At least at Sapporo (43° N. L.) I could not find the hibernation of the exules on *Sasa* by field observations made in spring. Especially, the spring appearance of alate exules seems very rare not only in the Japanese form of *P. morrisoni* but also in other Japanese eriosomatines. Thus, more detailed studies are needed to determine whether the distribution of *P. morrisoni* in North America is wholly artificial.

Tetraneura zelkovisucta Zhang, 1980, was described from globular galls on *Zelkova serrata* in southern China on the basis of only quantitative differences from *Paracolopha morrisoni*. It is, however, completely included within the variation range of the Japanese form (Table 2), thus should be regarded as the same species as *Paracolopha morrisoni*.

I could not find this species in Taiwan in spite of the abundance of *Zelkova* there. Mordvilko (1935, p. 131) briefly mentioned that in Taiwan the exule generations occur parthenogenetically on the roots of bamboos or other gramineous plants, although there may have been no reliable records of the species in Taiwan.

As mentioned by Akimoto (1983), *Watabura nishiyae* has nothing to do with this species and probably corresponds to a certain pemphigid species associated with *Malus pumila* and *Cydonia vulgaris*.

Fundatrix first instar larva (Fig. 1). Body elliptical, small, 0.523-0.597 (0.550) mm long, 0.41-0.49 (0.46) times as wide as long, wholly sclerotized except for the ventral surface. No wax gland plates present. Eyes with only 3 ommatidia. Antennae short, 4-segmented, smooth, not imbricated, 0.099-0.114 (0.107) mm long, 0.17-0.21 (0.19) times as long as body, 0.78-0.88 (0.83) times hind femorotrochanter length. Antennal segment IV somewhat elliptical, on the apical half tapering towards the primary rhinarium located at the apex, almost as long as segment III; processus terminalis indistinguishable. Antennal segment III rather roundish marginally, thicker to apex. Primary rhinarium acute apically, projecting as a horn, 0.006-0.008 mm long on segment III and 0.008-0.010 mm long on segment IV; that on IV with a few semicircular accessory rhinaria on the base. Antennal setae long and thick. Six setae present on segment IV; the apical one longest, rather blunt at the point, 0.051-0.064 mm long; the basal one conspicuously capitate, 0.041-0.051 mm long. Antennal segment III with 4 setae. Head and thorax divided symmetrically by a median, unsclerotized line on the dorsum. Cephalic setae pointed and short. Head on the dorsum with 1 pair of setae posteriorly, 1 pair laterally just above eyes, 1 pair medio-anteriorly, and 1 pair laterally just above antennal bases; on the frons with 1 pair; on the ventrum with 1 pair medio-anteriorly and with 1 or 2 facial setae. Rostrum reaching hind coxae; rostral segment II without a distinct transverse sclerotized band; ultimate segment smooth, convergent slowly with almost straight margins, with 10 setae, 0.67-0.73 (0.69) times hind femorotrochanter length. Legs smooth; tarsal segment I almost completely fused with segment II, with an unsclerotized spot basally. Dorso-apical and latero-apical setae on tarsus thick, capitate apically; the former 0.048-0.058 mm long in hind legs. Setae on tarsal segment I long, acute apically, 0.045 mm long. Empodial setae thicker apically, but not distinctly capitate, far exceeding the points of the claws, 0.025-0.030 mm long in hind legs. Tibia with thick, rather spine-like setae on apical half. Tergum more or less wholly sclerotized; thoracic and abdominal tergites distinctly demarcated by unpigmented intersegmental lines. Abdominal tergites VII and VIII slightly spinulose. Each tergite more weakly sclerotized along posterior margin. Body setae, except in the proximity of the posterior end, short and pointed. Pronotum anteriorly and posteriorly with 2 transverse rows each of 1 spinal and 1 pleural pair of setae; meso- and metanotum each with 2 lateral pairs, anteriorly and posteriorly, 1 pleural pair, and 1 spinal pair; abdominal tergites I-V each with 1 transverse row of 1 spinal, 1 pleural and 1 lateral pair; tergites VI and VII with 1 spinal and 1 lateral pair; tergite VIII and cauda each with 1 pair of setae. The setae on tergites VII and VIII and lateral ones of tergites V and VI conspicuously thick and long, with a more or less capitate point. Spinal setae on tergite III 0.006-0.010 mm long, and those on VII 0.025-0.043 (0.032) mm long. Thoracic sternites and abdominal sternite I without setae; abdominal sternites II-VII with 1 pair of spinal setae; sternite VIII with 4 setae. Thoracic and abdominal spiracles present ventrally, not upheaving, with a distinct rim round, 0.008-0.010 mm long in diameter. Biometric data shown in Table 9.

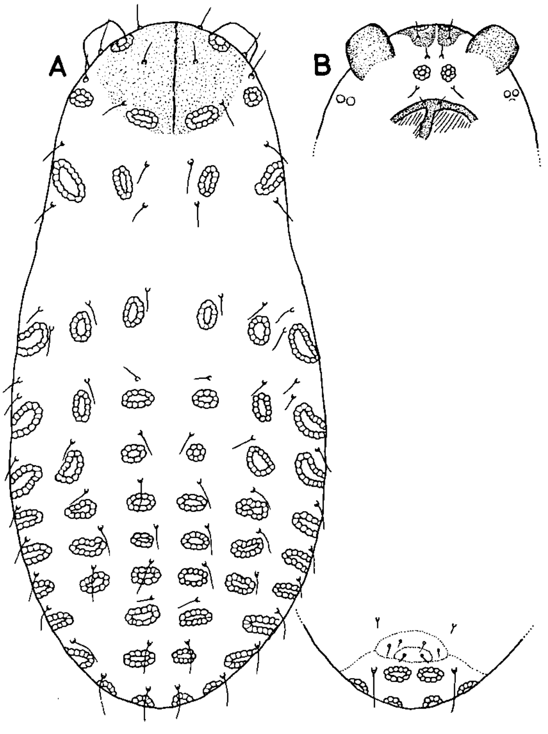

Fig. 3. *Paracolopha morrisoni* (Baker, 1919), first instar larva borne by the emigrant. A Dorsum, B Ventrum.

First instar larva borne by the emigrant (Figs. 3 and 4). Body elongate, 0.436-0.482 (0.453) mm long, 0.41-0.46 (0.43) times as wide as long, delicate and weakly sclerotized only in legs, antennae, rostrum, head and clypeus; with distinct wax gland plates scattered over. Eyes indistinct, hardly sclerotized, with 3 small ommatidia (usually only 2 ones are visible). Antennae short, 4-segmented, 0.095-0.101 (0.098) mm long, 0.20-0.23 (0.22) times as long as body, 0.85-0.95 (0.89) times hind femorotrochanter length. Antennal segments I and II smooth and cylindrical, and segments III and IV more or less roundish marginally, broader than I and II. Segment III almost as long as IV ; in the basal half becoming almost straightly thicker from the base, weakly sclerotized, showing slight imbrication with minute spinules scattered over ; in the apical half slightly roundish marginally, more strongly sclerotized with rather stout spinules. Segment IV basally rather roundish and broad, suddenly narrower to apex with nearly concave margins, with rather stout spinules scattered over, not imbricated. Primary rhinarium transverse in both of segments III and IV, with a circular opening, from which 2 semitransparent tonguelets extend to each lateral side, a little surrounding the segment, projecting as horns across margins. Tonguelets surrounded in a single line by dense cilia, which are longer and more densely arranged on posterior line. One accessory rhinarium present on IV, located almost opposite the primary one, with 1 clear opening from which a furcate tonguelet projects. Antennal setae long and acute. Antennal segment IV with 7 setae ; the apical one with a conspicuously projecting socket on the narrowly prominent apex, thick and the longest, 0.035-0.041 mm long. Antennal segment III with 4 setae. Head weakly sclerotized dorsally and frontally, with a median, unsclerotized line. Cephalic setae all acute and feeble ; on the dorsum 1 pair (S1) outside medio-posterior wax plates, 1 pair (S2) just anteriorly to latero-posterior wax gland plates, 1 pair (S4) medio-anteriorly, and 1 pair (S3) laterally just above antennal bases ; on the frons 1 pair (S5) anterior to dorso-anterior wax gland plates ; on the ventrum 1 pair (S6) medio-anteriorly and 2 pairs (S7, S8) just anteriorly and posteriorly to the facial wax plates. Rostrum very long, reaching to the proximity of the posterior end ; segment II weakly sclerotized basally and apically on the underside ; ultimate segment convergent almost staightly, sclerotized laterally, spinulose on the lateral sides of the surface and on the under surface, with 10 setae, 0.093-0.096 mm long, 0.83-0.91 (0.87) times hind femorotrochanter length.

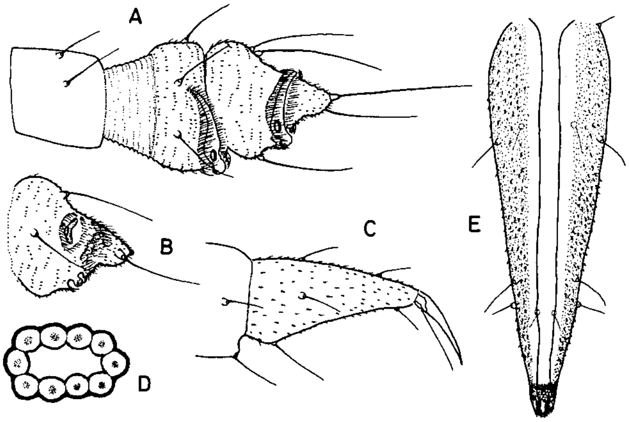

Fig. 4. *Paracolopha morrisoni* (Baker, 1919), first instar larva borne by the emigrant. A Antennal segments II-IV, B Antennal segment IV (opposite side), C Hind tarsus, D Spinal wax gland plate on abdominal tergite III, E Ultimate rostral segment.

Femorotrochanter and tibia smooth. Tibia 0.73-0.76 times femorotrochanter length in hind legs. Tarsus completely united, tapering with almost straight margins, rather coarsely spinulose; tarsal setae all simple, undeveloped; claws almost straight; empodial setae feeble, almost as long as claws. Tergum not sclerotized, not spinulose. Body setae all acute and feeble. Arrangement of dorsal and ventral body setae as in the fundatrix first instar larva. Spinal setae on tergite III about 0.01 mm long, and those on VII about 0.035 mm long. Wax gland plates elliptical to irregular and transverse-extended, slightly and regularly waving marginally, with a single row of circular cells, which surround a transverse central field; outer margin of circumferential cells more broadly rimmed than the inner. Individual cells darker in the centre than in the outer part. Central fields microscopically bright. Head with 5 pairs of wax gland plates; on the dorsum 1 pair (W1) along posterior margin of cephalic sclerite, 1 pair (W2) out of the sclerite near eyes, and 1 pair (W3) anteriorly; on the medio-frontal position 1 pair (W4); on the ventrum 1 pair (W5) anteriorly to clypeus. Pronotum with 2 pairs spinally and laterally. Meso- and metanotum and abdominal tergites I-IV each with 1 transverse row of 1 spinal, 1 pleural and 1 lateral pair. Abdominal tergites V-VII each with 1 spinal and 1 lateral pair, and tergite VIII with only 1 spinal pair. Lateral wax plates usually larger and more elongate than spinal ones on the same tergite. Spinal wax plates on tergite III 0.015-0.020 mm long in maximal length. Spiracles inconspicuous, without a distinct pore, not upheaving at all, not sclerotized. Biometric data shown in Table 12.

Exule adult (Figs. 5 and 6; Plate I A, B, C and D). Body rather elongate, posteriorly broadly rounded, membranous except for antennae, legs, rostrum and clypeus; creamy white, with white waxy secretion covering body wholly; 1.48-1.80 (1.66) mm long and 1.01-1.16 (1.07) mm wide, 0.61-0.70 times as wide as long; with wax gland plates scattered over. Pro- and mesothorax conspicuously elongate and apically narrower. Eyes small and indistinct, with 3 ommatidia only. Antennae short, variable in length, 5-segmented, rarely 6-segmented by the division of segment III (No. 9), not imbricated, 0.09-0.11 times body length (0.14 times for 6-segmented ones), 0.50-0.67 times hind femorotrochanter length (0.71 for 6-segmented ones). Antennal segment III slightly convex marginally or cylindrical, 0.65-0.92 times as wide as long, smooth, sometimes with an incomplete slit; segment IV conspicuously thicker apically with roundish margins, sometimes oval-shaped, 0.96-1.36 times as wide as long, often slightly with spinules; segment V with almost parallel or slightly convex margins, at apex

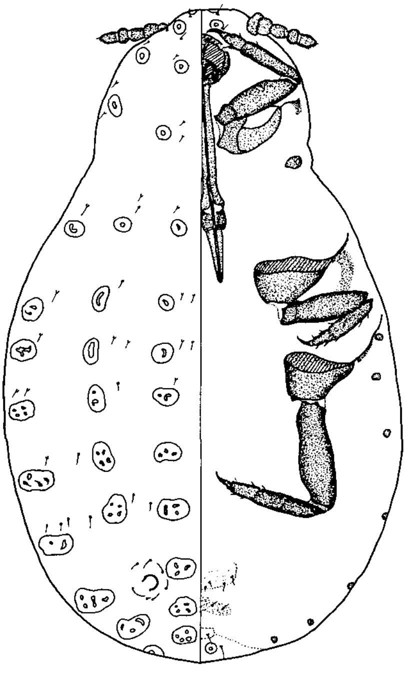

Fig. 5. *Paracolopha morrisoni* (Baker, 1919), exule adult. Right: Ventrum; Left: Dorsum.

truncated obliquely, thinly with transverse rows of spinules, more slender than segment IV, 0.56- 0.71 times as wide as long with undeveloped processus terminalis. Primary rhinarium represented by an opening from which a tonguelet projects, ciliated; on segment IV 2 short arms of the tonguelet projecting laterally from 1 opening; segment V with 2 openings, the larger one has 1 furcate tonguelet whose long arms extend anterio-obliquely, and the smaller one (accessory rhinarium) has 1 tonguelet. Antennal setae indistinct and all acute. Antennal segmant III without setae; IV with 2-4 setae; V on the basal half with 1-2 ones and on the apical half with about 5 setae in addition to shorter cilia. Head not sclerotized. Arrangement of cephalic setae quite as in the emigrant progeny. Rostrum often reaching middle coxae; segment II weakly sclerotized on basal 1/3 and apically; ultimate segment convergent almost straightly, sclerotized, not spinulose or very slightly with spinules along labial groove, with 10 inconspicuous setae, 0.42-0.53 (0.46) times hind femorotrochanter length. Femorotrochanter, tibia and tarsus smooth. Femorotrochanter broad, 0.25-0.30 times as wide as long. Tarsus completely united, without a slit; fore tarsus ventrally with a conspicuously enlarged setal socket on which 1 stout seta occurs, basally to the socket very thick with parallel margins, there about 0.55 times as wide as long; middle tarsus with a slight projection on ventro-basal position; hind tarsus with almost straightly convergent margins. Setae on tibia and tarsus stout, short, rather spine-like. Claws large, stout, sharply curved, 0.58-0.66 times tarsal length in hind legs; empodial setae invisible or extremely rudimentary. Body setae rather long, arranged in a row across each tergite; 0.04-0.05 mm long on the spinal position of abdominal tergite III. Wax gland plates nearly circular on head, circular to oval on thorax, rather irregular-shaped on abdomen, consisting of central field(s) and circumferential cells; the outer margin and the

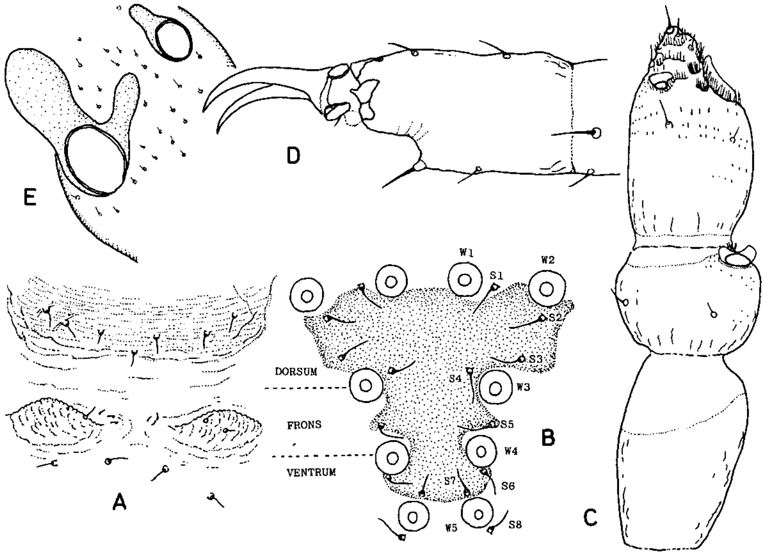

Fig. 6. *Paracolopha morrisoni* (Baker 1919), exule adult. A Genital and anal plates, B Cephalic setae and cephalic wax gland plates, C Antennal segments III-V, D Fore tarsus and claws, E Primary rhinarium (large) and accessory one (small) on antennal segment V.

margins of central fields dark rimmed. Head, pronotum, and mesonotum usually with 1 oval to strongly transverse central field, and metanotum and abdominal tergites usually with 2-5 fragmentary central fields in 1 plate (but sometimes there are individuals whose central fields are not fragmented in material collected from the same colony). Circumferential cells oval to drop-shaped, indistinctly rimmed, irregularly arranged in abdominal wax plates. Spinal and lateral wax gland plates on abdominal tergite III about 0.05 and 0.05-0.07 mm long, respectively, in maximal diameter. Arrangement of wax plates as in the emigrant progeny. Cornicles present on pleural position of tergite V, with a microscopically bright, horseshoe-shaped rim, slightly upheaving, not sclerotized around, thinly surrounded by 8-11 setae. Genital plate not sclerotized and so indistinct, with 7-10 setae along lateral and posterior margin. Anal plate comprising 2 gently upheaving lobes, each slightly sclerotized, altogether with 3-6 setae ; a set of 3-4 gonochaetae present anteriorly to each lobe. Abdominal sternite VIII with 1 transverse row of 4 setae, and cauda with 1 pair of setae. Biometric data shown in Table 17.

Emigrant adult (Fig. 7A). Body elongate oval, 1.35-2.36 (1.96) mm long, without wax gland plates. Head and thorax dark brown, and antennae and legs brown. Abdomen wholly membranous. Wings wholly shaded in brown, strongly so along veins. Antennae very short, 6-segmented but sometimes, in one side or both of the body, 5-segmented with an imperfect division between the original antennal segments III and IV, not imbricated and smooth except for processus terminalis of VI, slightly with longitudinal wrinkles all over, 0.39-0.53 mm long, 0.22-0.32 (0.25) times as long as body, 0.79-0.95 (0.84) times as long as hind tibiae. Antennal segment III relatively short, variable in length, 0.53-0.86 (0.73) times length of IV, V and VI combined. Segment IV rather oval in profile, 0.46-0.59 times as wide as long ; V almost as long as IV, roundish marginally, thicker towards subapical point, there 0.41- 0.60 times as wide as long ; VI slightly longer than V, more or less transverse oval in profile, with a depression at the primary rhinarium, 0.35-0.44 times as wide as long at maximum ; processus terminalis on VI stumpy, 0.015 mm long, rather obliquely projecting, showing slight imbrication, coarsely with minute spinules arranged in transverse rows, which stretch basally to reach the middle of the segment VI. Secondary rhinaria found on III-VI, narrow, thinly upheaving, microscopically represented as blight lines on dark pigmented background, covering usually 2/3 the circumference from the ventral side but sometimes with much shorter ones ; interrhinarial part not constricted ; the apical one of VI often connected to the next to form a X-shaped rhinarium. Primary rhinarium on segment V without an opening, not ciliated, always jointed with the apical secondary rhinarium which is more irregular in shape and sometimes thicker than other secondary ones ; that on VI partly ciliated, with an irregular-shaped "window", from which a semitransparent tonguelet projects anteriorly, and an issue of which is often connected with a secondary rhinarium, laterally accompanied by a few ciliated, semicircular accessory rhinaria. Antennal setae very short and scarce, present on the dorsal side, shorter than 0.01 mm long on segment V ; segment III usually without setae, if present with 1 or 2 ones, IV with 0-3, V with 1-4, VI with 1 at the base of processus terminalis and 4 thick ones at the apex, and further with 0-2 on the basal half. Segment III, if wanting in setae, with 1 or 2 tubercles, the abortive sockets of setae ; setal socket pale in contrast with dark background. Head ventrally with as many as 7 short setae on the furcate sclerite posterior to median ocellus. Rostrum short, not neatly reaching the middle of fore and middle coxae; ultimate rostral segment short, with gently convex margins, slightly spinulose, 0.097 mm long on the average, 0.71-0.84 times as long as the second segment of hind tarsi, with 5-8 short setae. Femorotrochanter short, 0.73-0.75 times tibial length in hind legs, slightly spinulose along hind margin. Tibia apically slightly spinulose. Tarsus with spinules neatly arranged in transverse rows; first segment with 2-2-2 setae, and without a spine-like seta; empodial setae rudimentary, far shorter than claws. Cornicles absent. Abdominal setae short, sparsely arranged in a single row across each tergite, 0.013-0.025 mm long spinally on tergite III and 0.030-0.049 mm long spinally on tergite VIII. Setae on sternites more densely arranged in single rows. Genital plate transverse, with transverse rows of denticles, without pigmentation, posteriorly with 18-28 setae strewn over. No distinct sclerites present laterally to genital plate. Anal plate forming 2 rather indistinct lobes, with 11-15 setae all over. One transverse row of 4 somewhat long setae of sternite VIII located just posteriorly to anal plate. Cauda semicircular, with 2 setae. Fore wings with unbranched media; the veins rather broad, not conspicuously bordered. Hind wings with only 1 oblique vein. Biometric data shown in Table 2.

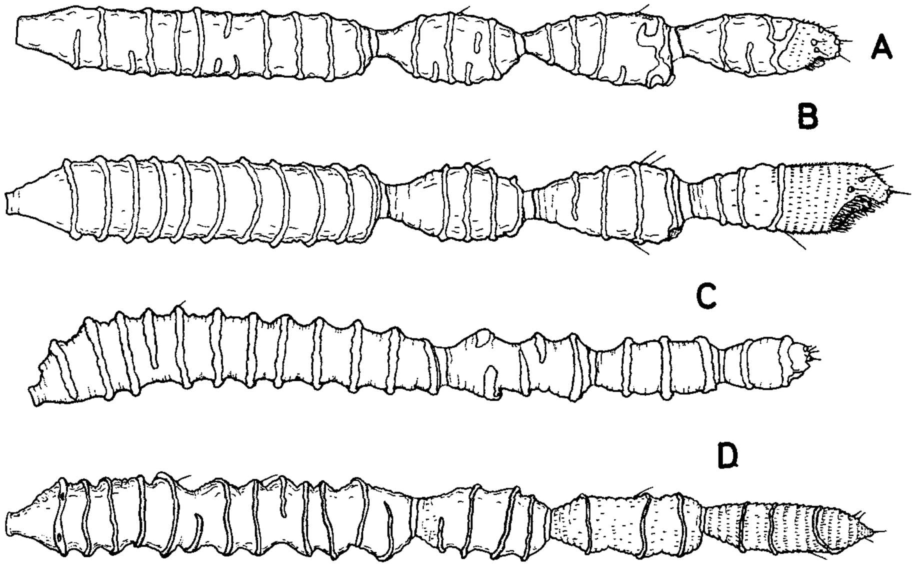

Fig. 7. Antenna. A: *Paracolopha morrisoni* (Baker, 1919), emigrant, B: Ditto, sexupara, C: *Colopha kansugei* (Uye, 1924), alate exule, D: *Kaltenbachiella elsholtriae* (Shinji, 1936), sexupara.

Sexupara adult (Fig. 7 B; Fig 12A). Since the sexupara is similar to the emigrant in many respects, the characters different between them and those indispensable for the identification will be especially referred to.

Body 1.63-2.21 mm long, without wax gland plates. Antennae longer than in the emigrant, 6-segmented, rarely 5-segmented in one of the pair with an imperfect division between the original segments III and IV, not imbricated and smooth except for the apical half of segment VI, slightly with longitudinal wrinkles, 0.48-0.68 mm long, 0.28-0.36 (0.31) times as long as body, 0.79-0.87 (0.82) times as long as hind tibiae. Antennal segment III relatively longer than in the emigrant, 0.74-0.97 (0.85) times length of segments IV, V and VI combined; IV rather oval in profile, 0.42-0.52 times as wide as long; V roundish marginally, thicker to the apex, there 0.44-0.54 times as wide as long; VI thicker towards the apical 1/3, more apically largely hollowed on the side of the primary rhinarium, 0.32-0.43 times as wide as long at apical 1/3, densely with conspicuous spinules arranged in transeverse rows, which expand basally across the middle of the segment. Primary rhinarium on segment VI densely fringed with much longer setae than in the emigrant, with a somewhat large tonguelet projecting anteriorly, not connected with the apical secondary rhinarium; a distinct circular opening present laterally to the primary rhinarium, without any projections. Secondary rhinaria more numerous than in emigrant in segment III. Antennal setae very short and scarce, present on the dorsal surface, 0.010- 0.015 mm long on segment V. Head ventrally with 5-7 setae over the sclerite posterior to median ocellus. Ultimate rostral segment more densely spinulose and longer than in the emigrant, convergent with almost straight margins, 0.96-1.16 times as long as the second segment of hind tarsi, with 5-8 setae. Characters on legs as in the emigrant except for empodial setae, which are longer and almost as long as claws. Abdominal tergites usually without sclerites, but when body is large, with a transverse spinal sclerite on tergite II. Cornicles present on the pleural position of abdominal tergite V, not upheaving, not sclerotized, each distinctly rimmed except for posterior or latero-posterior position, surrounded by 5-8 setae; diameter of the opening 0.015-0.020 mm long. Abdominal setae 0.020-0.040 mm long spinally on tergite III and 0.035- 0.045 mm long spinally on tergite VIII. Genital and anal plates as in the emigrant, with 21-28 and 12-14 (except for 4 setae on sternite VIII) setae, respectively. Biometric data shown in Table 3.

Fundatrix adult (Fig. 24 A). Body broadly rounded, without clearly bordered wax gland plates. Head and prothorax slightly projecting from rounded body. Legs short. Antennae narrow, 4-segmented, 0.10-0.12 times as long as body, 0.53-0.61 times hind femorotrochanter length; slightly with spinules on segment IV; segment III longest, a little thicker to apex; segment IV a little narrower to apex or almost parallel marginally, at apex with short projecting, horn-like primary rhinarium. Primary rhinarium not ciliated. Femorotrochanter slightly with spinules only along posterior margin. Tibia and tarsus smooth. Tarsus 1-segmented, slightly tapering. Rostrum reaching middle coxae; ultimate segment with convex margins. Spiracle plate circular, distinctly sclerotized. Appendages weakly sclerotized. Biometric data shown in Table 22.

Gall (Plate II B and C). Elongate, apically globular, straightly and slowly narrower to the basal point, without hairs, with thick wall, rough in the apical surface, almost in the same colour as the leaf.

Specimens examined. Fundatrix first instar larvae, all but No. 1 from young leaves of *Zelkova serrata*, No. 1, Sapporo, hatched in laboratory from an egg collected on a stem of *Z. serrata*; No. 2-10, Sapporo, 26-V-1984.

Fundatrix adults, all from galls on *Zelkova serrata*, No. 1 and 2, Palgon-san, Korea, 21-V-1982 (T. Fujisawa leg.); No. 3 and 4, Sapporo, Japan, 7-VII-1983; No. 5-7, Sapporo, 20-VI-1983.

Emigrants, all from galls on *Zelkova serrata*, No. 1-1~3, Sapporo, 7-VII-1983;

No. 2-1~4, Sapporo, 5-VII-1983; No. 3-1~5, Amanosan, Ôsaka Pref., 1-VI-1957 (Takahashi collection).

Emigrant progeny, all from emigrants collected on *Zelkova serrata*, No. 1-10, Sapporo, 5-VII-1983.

Exule adults, all from the roots of *Sasa* spp., No. 1-7, Sapporo, 26-IX-1983; No. 8-10, Sapporo, 27-IX-1980.

Sexuparae, No. 1 and 2, Bibai, Hokkaidô, on bark of *Ulmus davidiana* var. *japonica* (erroneously oriented), 17-X-1983 (Y. Yamaguchi leg.); No. 3, Sapporo, on the roots of *Sasa* sp., 27-IX-1980; No. 4, Sapporo, on bark of *Ulmus davidiana* var. *japonica*, 19-X-1980; No. 5, Nishinasuno, Tochigi Pref., on bark of *Zelkova serrata*, 17-X-1978 (S. Aoki leg.); No. 6 and 7, Kyôto Pref., ?-X-1957 (Takahashi collection); No. 8, Ôsaka Pref., on bark of *Zelkova serrata*, 23-XI-1959 (Takahashi collection).

Paracolopha takahashii sp. nov.

Remarks. The present species was found out of the mounted specimens of the Takahashi collection preserved in Hokkaidô University. The characteristics of the wax gland plates, tarsi and cornicles showed that the species has not been reported so far. Since the slide was in bad condition for observation, seven apterous forms included in it were cleaned by KOH, dyed by fuchsin and remounted to four slides. They were collected on the base of *Carex breviculmis* on 29 January by Dr. Sôrin.

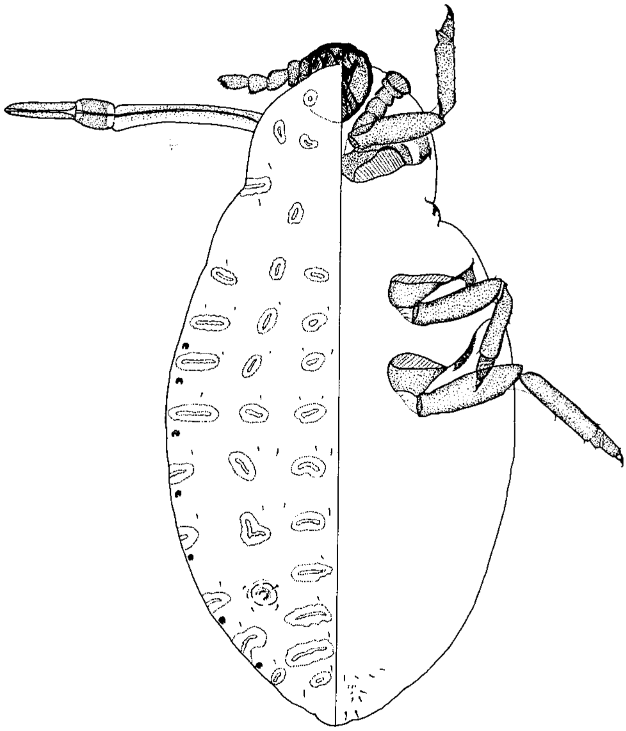

Fig. 8. *Paracolopha takahashii* sp. nov., exule adult. Right: Ventrum; Left: Dorsum.

Since then this species has not been rediscovered. It may permanently be passing an anholocyclic life-cycle on *Carex*, having no gall generation.

Exule adult (Figs. 8 and 9). Body elliptical, with a slight constriction between prothorax and mesothorax, membranous except for antennae, legs, rostrum and clypeus; 1.25-1.50 mm long and 0.52-0.53 times as wide as long; with indistinctly rimmed, though large, wax gland plates scattered over. Eyes larger than in the corresponding form of *P. morrisoni*, with 3 ommatidia. Antennae short, 5-segmented, not imbricated, 0.13-0.16 times body length, 0.76-0.98 times hind femorotrochanter length. Antennal segment III thicker apically, with almost straight or slightly convex margins, at the apex 0.77-1.0 times as wide as long, occasionally with minute spinules, often with an incomplete slit in the middle; segment IV thicker apically with almost straight or slightly convex margins, at the apex 0.88-1.27 times as wide as long, slightly with minute spinules; segment V with gently convex margins, with stumpy processus terminalis, widest at the middle, there 0.40-0.48 times as wide as long, more slender than segment IV. Primary rhinarium represented by an opening with projections, densely ciliated; segment IV with 1 opening from which a small furcate object projects; segment V with 2 openings, the larger one has 2 slender, capitated arms in the projection, and the smaller one (accessory rhinarium) is located next to the former and has no visible projections. Antennal setae very short and all acute. Antennal segment III without setae; IV with 2-3 setae; V on the basal half with 0-2 setae and on the apical half with 4-5 setae, in addition to shorter cilia. Head very slightly sclerotized dorsally and frontally. Cephalic setae all simple, and their arrangemint quite as in the corresponding form of *P. morrisoni*; on the dorsum 1 pair outside medio-posterior wax gland plates, 1 pair anteriorly to lateral wax gland plates, 2 pairs posteriorly to and inside anterio-lateral wax gland plates; on the frons 1 pair; on the ventrum 1 pair just posteriorly to medio-anterior wax plates, 2 pairs anteriorly and posteriorly to facial wax gland plates. Rostrum very long, apparently reaching hind coxae or exceeding them; segment II weakly sclerotized basally and apically; ultimate segment rather slowly convergent with straight margins, wholly sclerotized, not spinulose, with 9-11 extremely short setae, 0.54-0.65 times hind femorotrochanter length. Femur smooth or slightly spinulose along posterior margin; tibia and tarsus smooth. Femorotrochanter 0.22-0.30 times as wide as long. Tarsus separated into 2 non-functional segments by an unsclerotized line in every leg; first segment conspicuously enlarged especially in fore leg, with its margin diverging apically against dorsal margin; second segment straightly converging marginally. Maximal value of width/length in fore, middle and hind tarsus as follows: 0.57-0.69, 0.55-0.71, 0.46-0.55. Setae on first tarsal segment with a normal socket, arranged in 2-2-2. Tibial and tarsal setae simple and feeble. Claws short, 0.34-0.42 times tarsal length in hind legs; empodial setae rudimentary, invisible by low magnification microscopy. Body setae feeble, 0.023-0.025 mm long on the spinal position of abdominal tergite III. Wax gland plates elliptical to strongly and irregularly extended oval, rather weakly rimmed marginally, consisting of 1 transverse, slit-like central field and circumferential cells which surround the former in 1 row. Individual cells oval, rather broadly but dimmly rimmed, inside with many minute black points. Lateral wax gland plates much more transverse and larger than spinal and pleural ones except for tergite VII, containing much smaller cells in the side near the body margin. Head with 5 pairs

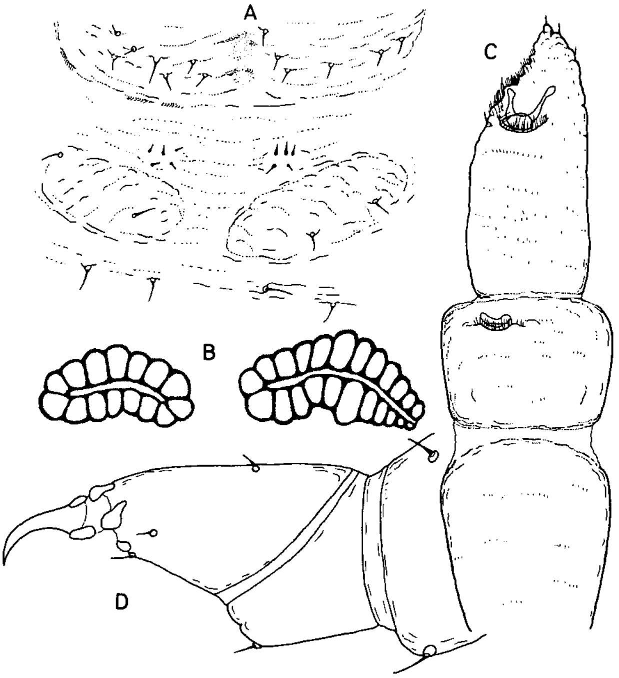

Fig. 9. *Paracolopha takahashii* sp. nov., exule adult. A Genital and anal plates, B Spinal (left) and lateral (right) wax gland plates on abdominal tergite VI, C Antennal segments III-V, D Fore tarsus and claws.

of wax gland plates; on the dorsum 1 pair oval (W1) medio-posteriorly, 1 pair transversely oval (W2) above eyes, 1 pair oval (W3) pleuro-anteriorly; on the frons 1 pair rather longitudinal (W4); on the ventrum 1 pair oval (W5) anteriorly to clypeus. Pronotum with 2 pairs spinally and laterally. Meso- and metanotum and abdominal tergites I-IV each with 1 transverse row of 1 spinal, 1 pleural and 1 lateral pair. Abdominal tergites V-VII each with 1 spinal and 1 lateral pair, and tergite VIII with only 1 spinal pair. Spinal and lateral wax gland plates on abdominal tergite III 0.03-0.05 and 0.06-0.09 mm long, respectively, in maximal length. Cornicles present pleurally on tergite V, without a sclerotized rim, which is represented only by a semicircular dark line, somewhat highly projecting, not sclerotized, thinly surrounded by 4-5 setae. Genital plate not sclerotized, dully represented, with 7-15 setae along posterior margin. Anal plate not sclerotized, comprising 2 very slightly upheaving parts, where altogether 4 or 5 setae present; a set of 4 or 5 gonochaetae present anteriorly to each part. Abdominal sternite VIII with 1 transverse row of 3 or 4 setae, and cauda with 3 or 4 setae. Biometric data shown in Table 18.

Specimens examined. Exule adults, No. 1-5 (No. 1 the holotype), Ôsaka Pref., ex *Carex breviculmis* subsp. *royleana* (base), 29-I-1956 (M. Sôrin leg., Takahashi collection).

GENUS COLOPHA MONELL, 1877

Diagnosis Alate—Body somewhat elliptical. Antennae 6-segmented, about 0.25- 0.30 times body length. Antennal segments V and VI, combined together, always shorter than III. Segments IV and V subequal, and VI almost equal to or rather shorter than V. Processus terminalis hardly projecting. Secondary rhinaria ring-like, arranged rather thinly on segments III-VI, not so highly projecting. Media of fore wing once branched. Hind wing with 1 oblique vein, but in *C. kansugei* additionally with 1 indistinct vein. Cornicles absent in the sexupara, and occasionally present in the emigrant merely as small pores. The furcate cephalic sclerite posterior to median ocellus with fewer than 10 setae. Abdomen dorsally with no sclerotized bands. Rostrum not reaching to the middle of fore coxae and middle ones; ultimate segment short, often roundish marginally. Genital plate arcuate posteriorly, but a little depressed along the median line to form 2 indistinct lobes, slightly pigmented along posterior margin or not, with setae along posterior margin. Anal plate also depressed in the central part, forming 2 lobes. Sclerotized plate absent in each side of genital plate.

Exule adult—Body broadly rounded or elliptical. Legs and antennae short. Legs mostly hidden under body when viewed from above. Antennae about 0.1 times body length, 4- or 5-segmented. Cornicles absent, or rarely present as small pores (*C. compressa*). Tarsus almost 1-segmented. Fore tarsus thickened, not tapering, with well developed setal socket at ventro-anterior position; the point of the socket exceeding the base of claws. Wax gland plates rather oval, arranged longitudinally in 6 rows, and reduced to 4 rows in abdominal tergite VII and to 2 in VIII; 1 central field and circular facets surrounding the former in 1 row present in 1 plate. Lateral wax gland plates rather larger, but not extended transversely. Body setae short, rather thinly distributed.

Exule first instar larva—Antennae 4-segmented. Primary rhinaria represented by 1 opening from which 2 short arms are directed to each lateral side.

Composition. In the list given by Eastop and Hille Ris Lambers (1976) the genus *Colopha* is recognized as consisting of the following eight species: *C. caucasica, C. clematicola, C. compressa, C. graminis, C. kansugei, C. moriokaensis, C. nirecola* and *C. ulmicola.* Of them, *C. caucasica* and *C. clematicola* have to be referred to another phylogenetic stock which has diverged on *Zelkova.* This stock at present includes *Hemipodaphis, Colophina* and *Byrsocryptoides* and is characterized, in gall generation, by distinctly bordered and granulated wax gland plates. *Colopha clematicola* is undoubtedly a member of *Colophina*, and *Colopha caucasica* should be placed near *Hemipodaphis* or included within it. In the present paper, *Colopha graminis* is regarded as a junior synonym of *C. kansugei*, and *C. moriokaensis* and *C. nirecola* are transferred to other genera. Consequently, the genus *Colopha* now consists of 3 known species, *C. compressa* occurring in Europe, *C. ulmicola* in eastern North America and *C. kansugei* in East Asia. In the biological aspects the first two species are characterized by their firm association with *Ulmus* species of the section *Blepharocarpus*, by their bag-shaped galls on intercostal regions of leaves, and by the occurrence of apterous fundatrigeniae (Mordvilko, 1935; Patch, 1910).

Gharesia polunini, the type species of the monotypic genus, is considered as a primitive member of the Tetraneurini (Stroyan, 1963). Its close relationship to *Byrsocryptoides* in morphology (Stroyan, 1963 ; Foottit and Mackauer, 1980), however, points to the possibility that *Gharesia* is a member of the above-mentioned phylogenetic group. The exule generation of *Gharesia* differs from that of *Colopha* in its wax gland plate lacking the central field and in its 2-segmented and not thickened fore tarsi. However, the primary host and the gall generations being not known, there remains uncertainty concerning the taxonomic position of the genus. For example, within *Kaltenbachiella*, the *K. nirecola* exule exceptionally has 2-segmented tarsi with the first segment not projecting, and the *K. elsholtriae* exule lacks wax gland plates on the abdominal tergites VII and VIII. The supposed position of *Gharesia* within the phylogenetic group is adopted with much emphasis on the structure and arrangement of its wax gland plates.

Colopha kansugei (Uye, 1924)

Eriosoma kansugei Uye, 1924, p. 410-411 〔originally described from Japan〕.

Truncaphis graminis Takahashi, 1930, p. 326-327 〔recorded from the Ryûkyû Islands〕. Syn. nov.

Colopha graminis : Takahashi, 1937, p. 207-208 〔redescribed〕.

Eriosoma kansugei : Higuchi and Miyazaki, 1969, p. 55 〔host〕.

Sinocolopha graminis : Tao, 1970, p. 138 〔recorded from Taiwan, and Fukien and Szechuan, southern China〕.

Colopha? kansugei : Eastop and Hille Ris Lambers, 1976, p. 160.

Colopha graminis : Eastop and Hille Ris Lambers, 1976, p. 160.

Colopha kansugei : Moritsu, 1983, p. 214 and p. 454 〔photograph and illustration〕.

Remarks. *Colopha graminis* has been recorded on the aerial parts of grasses in southern East Asia : the Ryûkyû Islands, Taiwan and southern China (Takahashi, 1930, 1937 ; Tao, 1970), while *Colopha kansugei* is known from southwestern Japan on the aerial parts of *Carex* spp. Although they well agree in the characteristics of wax gland plates of the apterous forms, there are quantitative differences in some features, especially in the antennae of the alates. *C. graminis* has 15-20 (usually 18) secondary rhinaria on the antennal segment III in material from Taiwan (Takahashi, 1937 ; Tao, 1970). *C. kansugei* differs in having much fewer ones (9-12) on the shorter segment. Recently I have had the opportunity to examine an aphid species collected on the stalks of *Carex* sp. in Nepal. This aphid well agrees with the Japanese *C. kansugei* almost in every respect, but is intermediate between the latter and the Taiwanese *C. graminis* in the number of the secondary rhinaria (12-16) on antennal segment III. I am therefore much inclined to believe that all these forms of *Colopha* belong to the same species.

Colopha kansugei, as here understood, has a wide range stretching from Nepal through China and Taiwan to southwestern Japan, with local populations differentiated in some quantitative characters. It should be emphasized that the Japanese and Nepalese forms completely agree in the larval characters. The primary host of *Colopha kansugei* has not been known. It may have become extinct in the areas where the aphid occurs, leaving parthenogenetic populations of the aphid on the secondary host plants. As mentioned later, *C. kansugei* may have once been associated with a member of the section *Blepharocarpus* of *Ulmus*. *Colopha kansugei* is quite similar to the American *Colopha ulmicola* in the biology on the secondary host. They form conspicuous colonies covered with much of waxy secretion on the aerial parts of grasses or Cyperaceae in autumn, but may also occur on the roots of those plants from spring to summer (Patch, 1910).

Exule first instar larva (Figs. 10 and 11). Body elongate, 0.578-0.737 (0.647) mm long, 0.36-0.42 times as wide as long (mean 0.40 in the Japanese form, and 0.39 in the Nepalese form); not sclerotized except for legs, antennae, rostrum, head and clypeus; with distinct wax gland plates scattered over. Eyes with 3 ommatidia and, in the space surrounded by them, with about 7-10 sclerotized tubercles. Antennae apparently 5-segmented; joint between segments III and IV non-functional, broadly not sclerotized. Antennal length 0.16-0.21 (0.18) times body length in the Japanese form, and 0.20-0.23 (0.21) times in the Nepalese form; 1.06-1.22 times hind femorotrochanter length. Antennal segments I and II smooth and cylindrical; segments III and IV seemingly continuous without constriction at the joint, cylindrical, almost equal in length and each 0.020-0.025 mm long; segment III smooth, without setae; segment IV with minute spinules scattered over, with 4 rather long, simple setae; segment V longitudinal conoid-shaped, with minute spinules scattered over, with 7 setae, the sockets of which are well developed. The seta on the sub-apex of segment V the longest, thick, rather blunt apically, on the average 0.034 mm long. Primary rhinarium present on segments IV and V, not transversely extended, represented by a circular opening from which a small, furcate object projects, only posteriorly and semicircularly surrounded by dense cilia; segment V with 2 or 3 ciliate accessory rhinaria, which are present laterally to primary one and have no projections. Head somewhat strongly sclerotized dorsally and frontally, with a median unsclerotized line. Cephalic setae simple and short; their arrangement quite as in the corresponding form of *Paracolopha morrisoni*. Rostrum reaching hind coxae; segment II, on underside, with 2 transverse, sclerotized belts at apical 1/3 and base; ultimate segment short, with apically strongly curved margins, sclerotized, on the surface slightly spinulose along labial groove, on the average 0.055 mm long, 0.44-0.53 (0.48) times hind femorotrochanter length. Four pairs of setae present on ultimate segment; on the surface 2 pairs anteriorly and posteriorly;

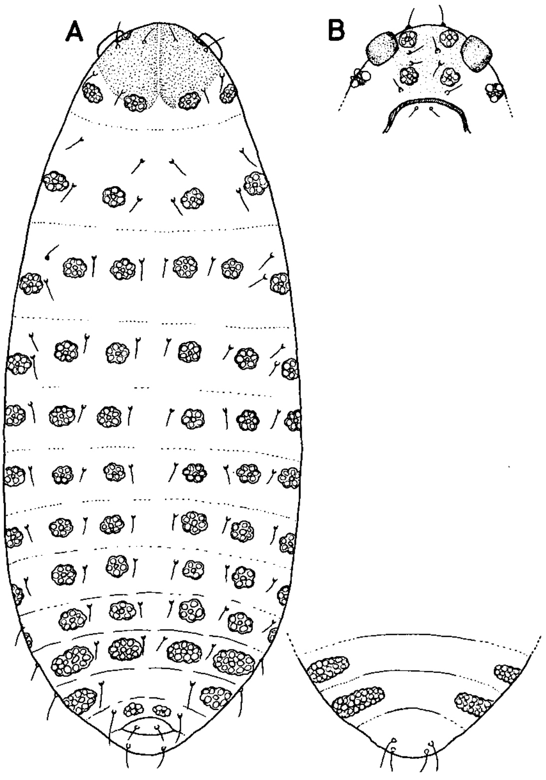

Fig. 10. *Colopha kansugei* (Uye, 1924), exule first instar larva. A Dorsum, B Ventrum.

latero-anteriorly 1 pair ; on the underside 1 pair anteriorly. Legs rather strongly sclerotized ; femur smooth, and tibia apically spinulose ; tibial length 0.82-0.89 times femorotrochanter length in hind legs. Tarsus basally with a rather pale, oblique slit or spot, but not completely separated ; with minute spinules, widest at basal 1/4, more apically tapering with gently convex margins ; with 1 pair of asymmetric dorso-apical setae, one of which is much thicker and longer with a capitated tip, and about 0.04 mm long, the other feeble. Empodial setae semitransparent, conspicuously spatulate, a little longer than claws. Claws also asymmetric, one being extremely reduced. Body setae all acute and feeble ; pronotum anteriorly and posteriorly with 2 transverse rows each of 1 spinal and 1 lateral pair of setae ; meso- and metanotum each with 2 lateral pairs, anteriorly and posteriorly, 1 pleual pair and 1 spinal pair ; abdominal tergites I-VI each with 1 transverse row of 1 spinal, 1 pleural and 1 lateral pair ; tergite VII with 1 pleural and 1 lateral pair ; tergite VIII with 1 lateral pair ; cauda with 1 short pair. Abdominal sternites II-VII each with 1 pair of spinal setae ; VIII with 2 pairs of rather long ones. Spinal setae on tergite III about 0.015 mm long and lateral ones on VIII about 0.025 mm long. Wax gland plates rather petal-shaped, distincly and broadly rimmed, consisting of a more broadly rimmed polygonal central field, which is occasionally partitioned into 2 parts, and circumferential cells. Cells circular, surrounding the central field in a single layer or partially multiplying to some layers ; weakly rimmed, with minute black points scattered over (number of cells in some wax gland plates are shown in Table 27). Central fields microscopically bright. Head with 5 pairs of wax gland plates, which are arranged as in the corresponding form of *Paracolopha morrisoni* ; on the dorsum 1 pair (W1) at the posterior margin of cephalic sclerite, and 1 pair (W2) laterally to this pair ; on the frons 1 lateral pair (W3) ; on the ventrum 1 pair (W4) medio-anteriorly, and 1 pair (W5) facially. Pronotum with 1 spinal and 1 lateral pair ; meso- and metanotum and abdominal tergites I-VI each with 1 transverse row of 1 spinal, 1 pleural, and 1 lateral pair, but on segments IV-VI lateral pair rather located on the ventral side ; abdominal segment VII with 1 dorso-lateral pair and 1 strongly transverse ventro-lateral pair ; tergite VIII with 1 pair of spinal wax plates having no central field. Spiracles inconspicuous, represented by minute holes. Biometric data shown in Table 13.

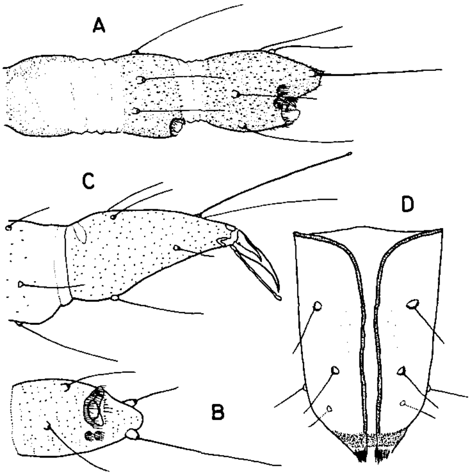

Fig. 11. *Colopha kansugei* (Uye, 1924), exule first instar larva. A Antenna, B Primary rhinarium on the apical antennal segment, C Hind tarsus, D Ultimate rostral segment.

Alate from the secondary host (Fig. 7C and Fig. 12B). Alate individuals were acquired on aerial parts of *Carex* spp. from both Japan and Nepal in autumn. The Japanese and Nepalese forms included in the abdomen sexuales and exule embryos respectively, thus corresponding with the sexupara and the alate exule. In spite of the difference in their life-cyclical positions, the two forms show slight quantitative differences only, so that they are described together, with special comments for the Nepalese form if necessary.

Body elongate oval, 1.46–1.70 (1.59, for the Nepalese form 1.57) mm long, without wax gland plates. Head, thorax, antennae and legs dark brown. Antennae short, 6-segmented but sometimes 5-segmented in one side of body by fusion of segments IV and V, not imbricated and smooth even in segment VI, 0.45–0.57 (0.51, for the Nepalese form 0.53) mm long, 0.29–0.36 (0.33) times as long as body, on the average 1.19 and 1.42 times as long as hind tibia, respectively, for the Japanese and Nepalese forms. Antennal segment III 1.16–1.36 (1.23, for the Nepalese form 1.27) times length of IV, V and VI combined ; proportion of IV, V and VI variable even among samples collected on the same plant, but usually IV longer than V, which is longer than VI ; segments IV and V more or less cylindrical, parallel marginally or slightly thicker apically ; VI shortened, rather oval in profile, 0.42–0.61 (0.52) times as wide as long. Processus terminalis on VI undeveloped, indistinct, without spinules, showing no imbrication, about 0.010 mm long. Secondary rhinaria present on III–VI, rather broad, about 0.005 mm wide, appearing as blight lines on dark background, usually covering about 2/3 the circumference on each segment from the ventral side ; interrhinarial part somewhat constricted ; the apical rhinaria on segment VI often very thick, widely covering the apical half except for processus terminalis ; no secondary rhinarium fused with neighboring one on every segment. Primary rhinarium on segment V without cilia, without an opening, always connected with the apical secondary rhinarium ; that on VI unciliated, with an inconspicuous semitransparent tonguelet, with a few semicircular accessory rhinaria fringed with short, inconspicuous setae, connected with the apical secondary rhinarium, forming a complicated shape. Antennal setae very short and scarce, typically 0.005 and at most 0.010 mm long on segment V ; III with 1–2 setae which are often reduced to small tubercles, IV without setae, V with 3 or 4 setae, VI on basal half with 0–2 setae and at reduced processus terminalis with 5 stout setae, which are at most about 0.010 mm long. Head ventrally with about 4 setae over the furcate sclerite posterior to median ocellus. Rostrum very short, ending far from the middle of fore and middle coxae ; ultimate rostral segment convex laterally, smooth, 0.060 mm long on the average, 0.67–0.80 (0.73) times as long as the second segment of hind tarsi, with 4–6 setae. Femorotrochanter short, in hind legs 0.83–0.86 times tibial length in the Japanese form and 0.93–0.97 in the Nepalese form, slightly spinulose along posterior margin ; tibia very short in comparison with femur or antenna, especially in the Nepalese form ; tarsus with transverse rows of spinules on the second segment, and the first segment also with spinules. Fore legs with conspicuously shortened second tarsal segment, 0.055–0.066 mm long, and with well-developed first tarsal segment, 0.030–0.040 mm long. First tarsal segment apically with 1 pair of setae in middle and hind legs, but in fore legs one located apically and the other subapically, the former thicker than the latter. Empodial seta conspicuously developed, spatulate apically, 0.020 mm long, much exceeding the points of the claws. Abdominal tergites without sclerites. Cornicles absent. Abdominal setae short, sparsely arranged in a single row on each tergite, about 0.020 mm long on tergites III and VIII ; setae on sternites more densely arranged. Genital plate unpigmented, rather depressed in the middle, forming 2 lobes, altogether with 18-21 setae, which mainly fringe the lobes. Pigmented plates absent laterally to genital plate. Anal plate also unpigmented, not distinctly divided into 2 lobes, wholly covered with 14-19 setae, from which the setae of sternite VIII are indistinguishable. Fore wings with once branched media ; hind wings with 2 oblique veins, basal one often inconspicuous. Biometric data shown in Table 4.

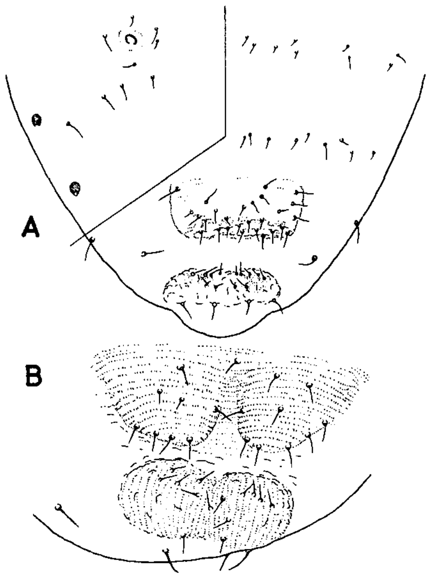

Fig. 12. Abdomen of sexupara. A : *Paracolopha morrisoni* (Baker, 1919) ; right, ventrum ; left, dorsum, B : *Colopha kansugei* (Uye, 1924), ventrum.

Exule adult (Fig. 13). Body elliptical, conspicuously tapering posteriorly, membranous, 1.25-1.56 (1.41) mm long and 0.49-0.65 (0.56) times as wide as long, with distinctly rimmed wax gland plates scattered over. Eyes with 3 ommatidia only. Legs and antennae extremely short, very weakly sclerotized. Antennae 5-segmented, variable in length and shape, not imbricated, 0.07-0.10 times body length, 0.71-0.96 times hind femorotrochanter length. Antennal segment III thicker apically with gently convex margins, sometimes with an unsclerotized slit at the middle, smooth, 0.69-1.10 times as wide as long at the apex ; segment IV shorter than III, with slightly convex margins, smooth, 0.98-1.30 times as wide as long ; segment V longer than IV, slightly spinulose, with slightly convex margins in the basal half, more apically rather straightly convergent to narrow processus terminalis when viewed from side (Fig. 13A, viewed from below), at base 0.50-0.70 times as wide as long. Primary rhinarium represented by a circular opening with a projection, not surrounded by setae ; that on segment IV with a small furcate object ; segment V with a slender, apically capitate one, additionally with about 3 ciliated semicircular accessory rhinaria. Antennal setae short ; segment III without setae ; IV with 4 setae ; V on the basal half with about 2 setae and on the apical half with 5 setae, one of which is present at the apex of processus terminalis. Head very weakly sclerotized, without a distinct median slit. Cephalic setae simple and short ; their arrangement is quite as in the exule first instar larva. Rostrum very short, reaching from the middle of fore and middle coxae to just middle coxae ; segment II weakly dark pigmented on the surface ; ultimate segment convergent with gently convex margins, subapically strongly curved, without spinules, with 8 setae, 0.29-0.45 times hind femorotrochanter length. Femorotrochanter slightly spinulose, and tibia and tarsus smooth. Tarsus completely united without a slit or very rarely with an incomplete one ; fore tarsus short, ventro-apically with a conspicuously prominent, oval-shaped setal socket whose seta is stout and a little shorter than claws, at base 0.68-0.91 times as wide as long ; middle tarsus with normal or slightly prominent setal socket at more basal position, at base 0.71-0.88 times as wide as long ; hind tarsus as in middle one, but longer, at base 0.53-0.75 times as wide as long. Dorso-apical setae

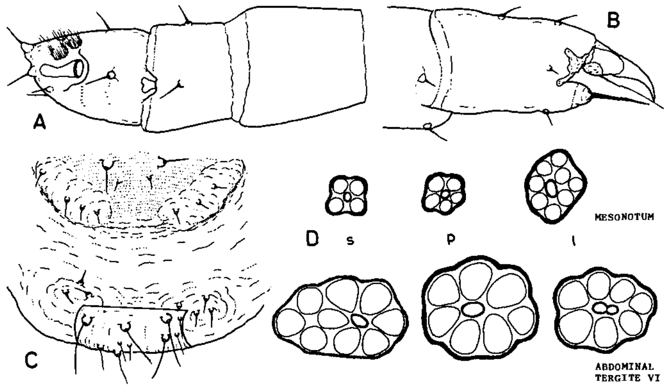

Fig. 13. *Colopha kansugei* (Uye, 1924), exule adult. A Antennal segments III-V, B Fore tarsus, C Genital and anal plates, D Wax gland plates; s-spinal plate, p-pleural plate, l-lateral plate.

on tarsus simple and fine. Setae on tibia and tarsus simple and fine. Claws short, 0.40-0.60 times tarsal length in hind legs; empodial setae spatulate at apex, a little exceeding the points of claws in all legs. Body setae arranged in a row across each tergite; usually 0.020-0.025 mm long on the spinal position of abdominal tergite III. Wax gland plate as in the exule first instar larva; but central field circular, black rimmed; circumferencial cells circular to oval, granulated. Arrangement of wax plates as in the exule first instar larva. Spinal and lateral wax gland plates on abdominal tergite III about 0.017-0.043 and 0.020-0.044 mm long, respectively, in maximal length. Cornicles absent. Genital plate not sclerotized, slightly upheaving along lateral margin; with 1 pair of long setae anteriorly and with 4-9 shorter setae laterally and centrally. Anal plate with 2 gently upheaving lobes, on which altogether 4-7 setae occur. About 10 long and short setae spreading over the surface above the lobes (ab. stern. VIII). Gonochaetae invisible or indistinguishable from other setae. Cauda semicircular, with 2 setae. Biometric data shown in Table 19.

Specimens examined. Exule first instar larvae, No. 1-7, Yamato, Kanagawa Pref., ex *Carex* sp. (aerial parts), 16-X-1980 (S. Aoki leg.); No. 8-13, Nagarjun nr. Kathmandu (1380 m), Nepal, ex *Carex* sp. (aerial parts), 12-X-1983 (S. Takagi leg.).

Apterous exule adults, No. 1-4, Yamato, Kanagawa Pref., ex *Carex* sp., 16-X-1980 (S. Aoki leg.); No. 5-8 (No. 8 the neotype), Ôsaka Pref., ex Cyperaceae, 3-XI-1961 (Takahashi collection; remounted); No. 9-11, Nagarjun nr. Kathmandu, Nepal, ex *Carex* sp., 12-X-1983 (S. Takagi leg.).

Sexupara adults, No. 1-3, Yamato, Kanagawa Pref., ex *Carex* sp., 16-X-1980 (S. Aoki leg.); No. 4 and 5, Ôsaka Pref., ex Cyperaceae (root), 23-XI-1955 (Takahashi collection).

Alate exule adults, No. 1-5, Nagarjun, nr. Kathmandu, Nepal, ex *Carex* sp., 12-X-1983 (S. Takagi leg.).

GENUS KALTENBACHIELLA SCHOUTEDEN, 1906

Diagnosis. Alate—Body somewhat elliptical. Antennae 6-segmented, often 5-segmented by the fusion of original segments III and IV, about 0.4 times as long as body. Antennal segment V always longer than IV (in a few species conspicuously longer); segment VI longer than or as long as V. The combined length of segments V and VI largely superior to the length of segment III (or identical with the latter in the *K. elsholtriae* sexupara). Processus terminalis of antennal segment VI hardly projecting. Secondary rhinaria very narrow, linear and compactly arranged on segments III-VI, often highly projecting. The furcate cephalic sclerite posterior to median ocellus with 10-20 setae. Media of fore wing simple, but once branched in *K. nirecola*. Hind wing always with 2 oblique veins. Cornicles unstable in appearance; *K. nirecola* always with ones that are sclerotized round the pore, but other species occasionally with 1 or 2 reduced ones. Abdomen dorsally without sclerotized transverse bands. Rostrum a little exceeding fore coxae. Ultimate rostral segment short, showing rather strongly convex margins. Genital plate curved posteriorly, somewhat sclerotized along hind margin, with setae posteriorly; 1 pair of long setae absent in the central part. Anal plate transverse, often forming 2 weakly sclerotized lobes. A dark pigmented plate present in each lateral side of genital plate.

Fundatrix first instar larva—Antennae 4-segmented. Primary rhinarium projecting anteriorly like a horn. Tergum not wholly sclerotized. Spiracle pore marked, present on dorsal surface in abdomen.

Fundatrix adult—Body broadly rounded. Antennae 4-segmented. Cornicles absent.

Exule first instar larva—Antennae 4-segmented. Primary rhinarium represented by an opening, from which 2 tonguelets extend to both lateral side. Tarsus spinulose and tapering. Claws almost straight.

Exule adult—Body broadly rounded. Head and posterior tip neither projecting nor becoming narrower. Antennae 4- or 5-segmented, and 0.10-0.13 times as long as body. Cornicles absent. Legs short and mostly hidden under body when viewed from above. Tarsus clearly separated into 2 segments or partly with a membranous, oblique slit. Second segment of tarsus more or less tapering. First segment of fore tarsus often thickened and projecting anteriorly, apically with 1 seta, the socket not reaching the base of claws. Wax gland plates arranged in 6 longitudinal rows, and reduced to 4 rows in abdominal tergite VII and 2 in abdominal tergite VIII. Lateral wax gland plates strongly transverse, but not clearly so in *K. elsholtriae*. Wax gland plate consisting of a central field and small circular facets surrounding the former, but in *K. spinosa* central fields separated into some irregular narrow spaces. Rostrum reaching middle coxae or scarcely so.

Composition. This genus consists of the following 8 species: *K. pallida* distributed from Europe to central Asia; *K. ulmifusa* in eastern North America; *K. japonica, K. spinosa, K. elsholtriae* and *K. nirecola* in East Asia; *K. glabra* in the mountain region of Taiwan; *K. carpinicola* in northern India. Eastop and Hille Ris Lambers (1976) assigned *nirecola* to *Colopha*. However, the pouch gall formed on the leaf midrib and the emigrant antennal characters of this species completely conform to the diagnostic characters of *Kaltenbachiella.*

Kaltenbachiella japonica (Matsumura, 1917)

Gobaishia japonica Matsumura, 1917, p. 75-76 〔originally described〕.
Gobaishia japonica : Monzen, 1929, p. 24-25 〔record from northern Honshû〕.
Gobaishia japonica : Mordvilko, 1935, p. 116-119 〔record from Vladivostok, USSR〕.
Gobaishia japonica : Shinji, 1941, p. 1065-1066.
Kaltenbachiella japonica : Börner and Heinze, 1957, p. 293-294 〔short remark〕.
Kaltenbachiella japonica : Hille Ris Lambers, 1967, p. 88 〔inference on the biology〕.
Kaltenbachiella japonica : Higuchi and Miyazaki, 1969 p. 55 〔host〕.
Kaltenbachiella japonica : Eastop and Hille Ris Lambers, 1976, p. 232.
Kaltenbachiella japonica : Sôrin, 1977, p. 7.
Kaltenbachiella japonica : Ghosh, 1981 〔redescribed〕.

Remarks. The globular spiny galls of the present species have arrested attention of several aphidologists, but little has been known about its peculiar biology. On the basis of material sent from Japan, Hille Ris Lambers (1967) first suggested that the alates which appear from the galls are sexuparae and that the species completes its cycle on the primary host. My repeated observations approved his suggestion, so that the recorded secondary host is apparently due to confusion with other species. The galls are mainly found on moderately aged or old rather than young elm trees and concentrated on particular portions of such trees, especially on shoots growing directly from trunks. In the campus of Hokkaidô University there are certain trees preferred by the aphid every year, with the infested twigs hanging down owing to crowded galls. In the portions on which galls are concentrated, the leaves may harbour four or more galls arranged linearly on the midrib, and are often distorted and partially withered, while almost all other leaves of the same trees remain free from galls. When galls occur crowded on one leaf, they are appressed together in a cluster (Plate IIID), while in the galls occurring singly the spine-like projections on them tend to become stouter. The alate aphids (sexuparae), which emerge from galls in late July to early August in Sapporo, may mostly move to the trunk close to their crowded colonies instead of flying away (Aoki and Yamaguchi, personal communication) and bear sexuales in the crevices of the trunk. As a result the breeding population may be concentrated on restricted parts of the trunk, on which therefore the eggs are also concentrated more or less. The eggs stay in dormancy from summer until the next spring and the hatched fundatrix larvae again form crowded galls on near twigs. Thus, patch-like distribution, not only among trees but also within a tree, results apparently from the philopatric habit of the sexuparae. Of course, young trees, as they grow, occasionally become colonized probably from near infested trees. The present species is very common throughout Hokkaidô, but it is uncertain whether it also occurs in other islands of Japan.

The type of life cycle represented by *K. japonica* is very rare in the Eriosomatinae, and is found only in another species, *Georgiaphis ulmi* (Börner and Heinze, 1957). A conspicuously concentrated distribution of its galls was reported by Hottes and Frison (1931). Mordvilko (1935) recorded the "emigrant" of *K. japonica.* This record should be revised by examining the embryos of the alate form.

Fundatrix first instar larva (Fig. 2). Body elliptical, very small, 0.411-0.461

(0.439) mm long, 0.44-0.49 (0.47) times as wide as long, membranous except for head, rostrum, appendages, clypeus, and some fragmented plates on dorsum. No wax gland plates present. Eyes well sclerotized, only with 3 ommatidia. Antennae extremely short, 4-segmented, smooth, not imbricated, 0.061-0.076 (0.067) mm long, 0.13- 0.18 (0.15) times as long as body, 0.71-0.88 (0.79) times hind femorotrochanter length. Antennal segment IV longer than III, apically roundish, subapically with a primary rhinarium projecting anteriorly like a horn ; primary rhinarium 0.010-0.012 mm long, accompanied by a few minute accessory rhinaria ; processus terminalis indistinguishable. Antennal segment III thicker to apex, there with a primary rhinarium similar, though shorter, to that of IV. Antennal setae all pointed ; segment IV with 7 setae, the apical one thickest, longest, and 0.046-0.051 mm long, sometimes additionally with 1-2 extremely short setae ; segment III with 3 setae shorter than on IV. Head dorsally covered with a broad sclerite divided symmetrically by an unsclerotized, median line, with 7 pairs of setae ; on the dorsum 1 pair posteriorly, 1 pair laterally just above eyes, 1 pair medio-anteriorly ; on the frons 1 pair laterally just above antennal bases, 1 pair somewhat below and inside the former (medio-frontally) ; on the ventrum 1 pair medio-anteriorly, 2 pairs facially. Rostrum reaching hind coxae ; rostral segment II with a transverse sclerotized band at the middle on the under surface, smooth ; ultimate segment smooth except for labial groove, marginally broadly convex on basal 1/3 of the segment and almost straight more apically, with 10 setae, 0.67-0.75 (0.71) times hind femorotrochanter length. Legs wholly smooth ; tarsus partially segmented by an unsclerotized line, with 1 pair of thick and capitate dorso-apical setae, which are 0.033-0.035 mm long in hind legs, and with also capitate latero-apical setae ; empodial setae spatulate, much longer than claws. Dorsum not wholly sclerotized ; each of pro-, meso- and metanotum laterally with 1 pair of polygonal sclerites ; pronotum additionally with 1 median sclerite divided symmetrically by a median line. Body setae simple, not enlarged towards posterior end, about 0.007 mm long. Lateral sclerites on each notum each with 2 setae. Median sclerite on pronotum with 2 pairs of setae anteriorly and posteriorly. Meso- and metanotum each with, between lateral sclerites, 1 transverse row of 1 pleural and 1 spinal pair of setae. Abdominal tergites I-V each with 1 transverse row of 1 spinal, 1 pleural and 1 lateral pair ; tergites VI and VII, respectively, with 1 transverse row of 5 and 4 setae ; tergite VIII and cauda each with 1 pair. Thoracic sternites and abdominal sternite I without setae. Abdominal sternites II-VII spinally with 1 pair ; sternite VIII with 4 setae. Thoracic and abdominal spiracles located ventrally and dorsally, respectively, slightly projecting, with a conspicuously large pore, which is about 0.01 mm long in diameter and surrounded by a small transverse sclerite. Biometric data shown in Table 10.

Sexupara adult (Fig. 17A and B ; Fig. 18B). Body elongate oval, 1.39-1.72 (1.55) mm long, without wax gland plates. Antennae relatively short, usually 6-segmented, but in one locality (Ônuma) often less segmented with abortive division(s) (of 20 antennae in 10 emigrants, 30% 4-segmented, 50% 5-segmented and 20% 6-segmented), 0.47-0.57 (0.51) mm long, 0.31-0.38 (0.34) times as long as body, 0.96-1.09 (1.04) times hind tibial length, rather thick, with segments V and VI long relatively to segment III, not imbricated. Antennal segments I-V smooth ; segment VI sparsely with spinules arranged irregularly over apical half ; processus terminalis not segmented by imbrication. Antennal segment III relatively short, 0.45-0.55

(0.50) times the combined length of IV, V and VI ; IV short, about 0.5 times as wide as long except for the width of secondary rhinaria ; V parallel marginally except for the base, 0.26-0.35 times as wide as long, at base thicker to the basal secondary rhinarium located at about basal 1/6 of the segment ; VI slender, parallel marginally, 0.20-0.26 times as wide as long; processus terminalis on segment VI stumpy, about 0.015 mm long. Secondary rhinaria present on segments III-VI, arranged densely, very narrow, about 0.0025 mm wide, strongly projecting on every segment, conspicuously winding especially on dorsal side, sometimes bifurcating or fusing with the neighboring ones to form a H-shape ; usually covering 3/4-4/5 the circumference, but variable in length, with extremely short or long one within a segment, not appearing as bright lines. Primary rhinarium on segment V without an opening, not ciliated, joined with a secondary rhinarium ; that on segment VI without a distinct opening, ciliated, without a tonguelet-like projection, connected with the apical secondary rhinarium of segment VI, with a few ciliated, circular accessory rhinaria. Antennal setae short and scarce, 0.014-0.025 mm long on segment V ; III with 2-4 setae ; IV with 0-3 setae ; V with 3-4 setae ; VI but processus terminalis with about 2 setae ; processus terminalis with 5 thick setae, the longest one of which is usually 0.014 mm long. Head ventrally with 12-22 setae on furcate sclerite posterior to median ocellus. Rostrum very short, a little exceeding fore coxae ; ultimate rostral segment slightly spinulose, convex marginally, 0.071-0.086 (0.078) mm long, 0.63-0.76 times as long as second segment of hind tarsus, with 7-10 setae. Femorotrochanter, in hind legs, very slightly spinulose (often indistinct) along posterior margin, 0.74-0.80 (0.77) times tibial length ; tarsus with transverse rows of spinules. First tarsal segment usually with 1 pair of long setae and sometimes also with 1 shorter, spine-like seta, (this frequently absent). Empodial seta feeble, a little exceeding the points of claws. Dorsum without intersegmental bands of sclerites in abdomen. Cornicles usually absent, each being a trace of a minute sclerite ; present on both sides in 1 specimen (No. 9) and on one side in another (No. 10), occurring laterally on segment VI, hardly upheaving, sclerotized narrowly round the opening, not surrounded by setae. Abdominal setae short and dorsally sparse, 0.020-0.030 mm long spinally on tergite III and 0.025-0.035 mm long at the longest on tergite VIII. Setae on sternites more densely arranged in single rows. Genital plate posteriorly arcuate, transverse, weakly pigmented, with 20-35 setae mainly scattered posteriorly, partly expanding to the central field. Dark pigmented, small, transverse plates present laterally to genital plate. Anal plate weakly pigmented, often forming 2 lobes, altogether with 19-29 setae, of which 10-13 ones are located in the anterior position. Cauda semicircular, with 5-14 setae. Fore wings with a simple media ; the veins as in *K. nirecola*. Hind wings with 2 oblique veins (Cu1a and Cu1b), but rarely once branched in Cu1a. Biometric data shown in Table 5.

Fundatrix adult (Fig. 24B). Body broadly rounded, without clearly bordered wax gland plates. In margins head continuous to rounded body. Legs short, almost hidden under the body in dorsal view. Antennae 4-segmented, 0.08-0.11 times as long body, 0.51-0.63 times hind femorotrochanter length ; wholly smooth ; segment III longest, thicker to the apex, with slightly convex margins ; segment IV convex marginally, at apex with short projecting primary rhinarium. Femorotrochanter slightly spinulose along posterior margin. Tibia and tarsus smooth. Tarsus incompletely separated to 2 segments. Rostrum reaching to the middle of fore coxae and hind ones; ultimate segment with straight or slightly convex margins, converging with narrow angle. Spiracle plates small and indistinct. Appendages weakly pigmented. Biometric data shown in Table 23.

Gall (Plate IIIC and D; Plate IVA) Projecting upwards from the midrib, globular, covered with fine spine-like projections, green but paler than the leaf, without hairs, thick in the wall. On the midrib, the part on which the gall occurs bends downwards.

Specimens examined. Fundatrix first instar larvae, No. 1-10, hatched in laboratory from eggs collected on the bark of *Ulmus davidiana* var. *japonica*, Sapporo, 1984.

Fundatrix adults, No. 1-4, Ônuma, Hokkaidô, ex galls on *Ulmus davidiana* var. *japonica*, 6-VIII-1983; No. 5 and 6, Sapporo, ex galls on *Ulmus davidiana* var. *japonica*, 23-VII-1983.

Sexuparae, No. 1-6, Ônuma, Hokkaidô, ex galls, 6-VIII-1983; No. 7, 8 and 12, Sapporo, 1-VIII-1960 (Takahashi collection); No. 9-11, Sapporo, ex galls on *Ulmus davidiana* var. *japonica*, 20-VII-1984; No. 13 (neotype) and 14, Sapporo, ex galls on *Ulmus davidiana* var. *japonica*, 23-VII-1983.

Kaltenbachiella spinosa sp. nov.

Remarks. The present species was first recognized as a new chromosomal race of *Kaltenbachiella japonica*. Neither characteristics of galls nor the diagnostic characters of gall-generations distinguish this species clearly from *K. japonica*. Further, their chromosome numbers ($2n=16$ in *K. japonica* and $2n=18$ in *K. spinosa*) show that the two species are more closely related to each other than to other *Kaltenbachiella* species (Akimoto, unpublished data). *Kaltenbachiella spinosa*, however, differs definitely from *K. japonica* in that the alate individuals emerging from the gall are "emigrants", having embryos of the exule-form. Thus, *K. spinosa* is heteroecious, having unknown secondary host. It is remarkable that morphologically *K. japonica* most closely approaches *K. spinosa* in the gall generation. Concerning the characters of wax gland plates, the sexupara larva of *K. japonica* corresponds with the emigrant larva of *K. spinosa* (Fig. 14), whereas probably differing from the latter's sexupara larva. The characters of wax gland plates in the

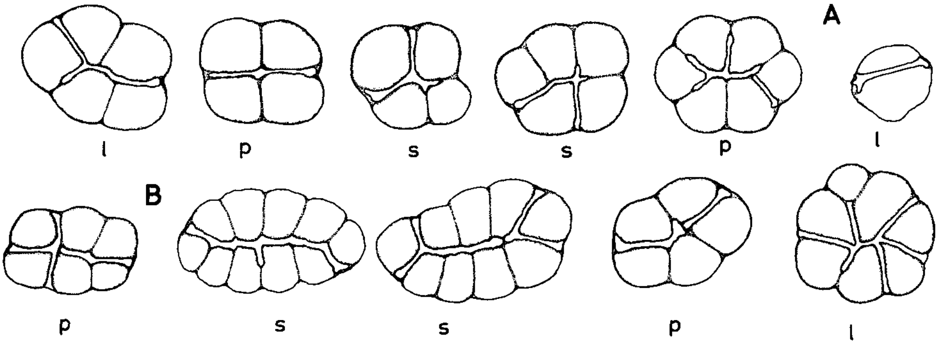

Fig. 14. Wax gland plates of 4th instar larva occurring in the gall. A: *Kaltenbachiella spinosa* sp. nov., on abdominal tergite VI, B: *K. japonica* (Matsumura, 1917), on abdominal tergite IV. s-spinal plate, p-pleural plate, l-lateral plate.

sexupara larvae of *K. spinosa* can be evaluated from the larvae deposited by the emigrant. These larvae have dimorphic wax gland plates between the lateral row and the spinal-pleural row (Fig. 15). The dimorphic pattern does not occur in the sexupara larvae of *K. japonica*. *K. spinosa* is recorded in central Honshû (Tsumagoi, Gumma Pref.) and central Hokkaidô (Bibai and Tôbetsu). In Hokkaidô the galls of this species are very rare even in the recorded habitats. The distributional relationship between *K. spinosa* and *K. japonica* has not been clarified enough, but within one locality (Tôbetsu) I found galls of the two species on different trees of *Ulmus davidiana* var. *japonica*. In contrast with the occurring pattern of the *K. japonica* galls, the galls of *K. spinosa* are not concentrated on particular parts of an elm tree and usually occur solitarily on the leaves. The galls of *K. spinosa* generally have stouter and more roughly arranged spines. However, this characteristic may not be reliable for the identification of *K. spinosa*, because the galls of *K. japonica* show a large phenotypic variation. It seems that the emigrant of *K. spinosa* is most clearly distinguished from the sexupara of *K. japonica* by having large values of antennal length relative to hind tibial length (1.23-1.38 vs. 0.96-1.09). However, more samples from various localities are needed to know whether the value can be regarded as a reliable recongnition character or not. The speciation and distribution of *K. spinosa* and *K. japonica* will be considered in detail in another paper.

First instar larva borne by the emigrant (Fig. 15 and Fig. 16). Body elongate, 0.393-0.441 mm long, 0.44-0.49 times as wide as long, sclerotized only in legs, antennae, rostrum, head and clypeus, with somewhat indistinct wax gland plates. Eyes as in the corresponding form of *Kaltenbachiella nirecola*. Antennae 4-segmented, 0.112-0.121 (0.116) mm long, 0.26-0.30 times as long as body, 1.10-1.19 times hind femorotrochanter length. Antennal segments I and II smooth and cylindrical; segment III thicker apically with broadly convex margins, on apical half coarsely with spinules arranged in rows; segment IV roundish marginally, not tapering with hardly prominent processus terminalis, rather coarsely spinulose. Primary rhinarium similar to that of *Kaltenbachiella nirecola*, but larger relative to the segment. Antennal setae long, simple. Antennal segment IV with 7 setae; the longest present at the apex of processus terminalis, 0.043-0.046 mm long. Antennal segment III with 4 setae only on apical half. Head weakly and broadly sclerotized, with a finely waving, median line. Cephalic setae simple; their arrangement quite as in the corresponding form of *Paracolopha morrisoni*. Rostrum reaching hind coxae; segment II weakly sclerotized over apical half on the underside, spinulose; ultimate segment broadly convex over basal half and straightly convergent over

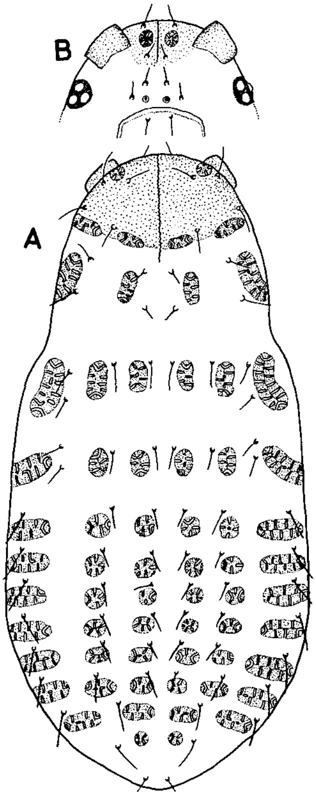

Fig. 15. *Kaltenbachiella spinosa* sp. nov., first instar larva borne by the emigrant. A Dorsum, B Ventrum.

apical half, spinulose except for labial groove, with 10 setae, 0.62-0.66 (0.64) times hind femorotrochanter length. Femorotrochanter smooth; tibia thinly with stout spinules mainly over apical half. Tarsus completely united, tapering, dorsally with slightly convex margin and ventrally with slightly concave margin, densely with stout spinules; claws straight; empodial setae blunt apically or slightly capitate, feeble, a little exceeding the points of claws. Dorsum not sclerotized, distinctly with transverse rows of denticles in cauda and abdominal segment VIII. Body setae simple and short; 0.01 mm long spinally on tergite III and 0.018-0.020 mm long on VIII. Arrangement of body setae as in the corresponding form of *Kaltenbachiella nirecola*. Wax gland plate dully represented, oval in spinal-pleural position, and strongly extended in lateral position; lateral one on thorax longitudinal and on abdomen transverse; narrowly dark rimmed, not waving marginally, without a central field, which disperses into some intercellular spaces as "canals". Cells irregularly shaped owing to dispersed central field, darker than the latter, with some black spots. Arrangement of wax gland plates almost as in *Kaltenbachiella nirecola*, but on head W4s located just posteriorly to S5s, not to S6s. Biometric data shown in Table 14.

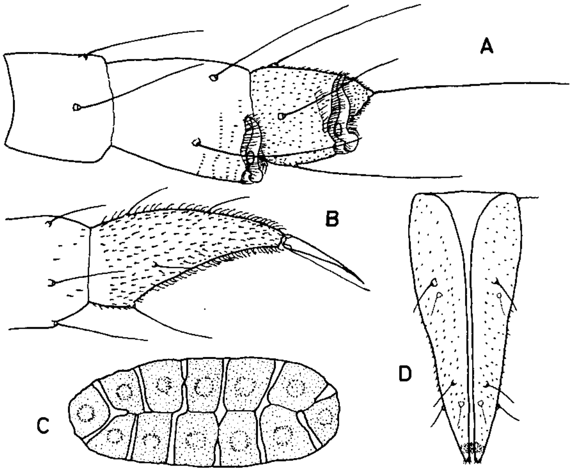

Fig. 16. *Kaltenbachiella spinosa* sp. nov., first instar larva borne by the emigrant. A Antennal segments II-IV, B Hind tarsus, C Lateral wax gland plate, D Ultimate rostral segment.

Emigrant adult (Figs. 17C and 18A). Body 1.00-1.40 (1.26) mm long, without wax gland plates. Antennae 6-segmented, but rarely 5-segmented by fusion of the original segments III and IV, 0.44-0.63 (0.54) mm long, 0.39-0.48 (0.42) times as long as body, 1.23-1.38 (1.30) times hind tibial length, with segments V and VI long relatively to segment III, not imbricated. Antennal segments I-V smooth; segment VI very sparsely with spinules arranged irregularly over apical 1/3 of the segment. Antennal segment III relatively short, 0.47-0.61 (0.54) times combined length of IV, V and VI; IV short, 0.34-0.50 (0.42) times as wide as long except for the width of secondary rhinaria; V becoming narrower to the base from the basal secondary rhinaria located at about basal 1/8 of the segment, more apically with parallel margins, 0.20-0.26 (0.24) times as wide as long; VI constricted basally with almost parallel margins, 0.20-0.24 (0.22) times as wide as long; processus terminalis almost as in the sexupara of *K. japonica*. Primary and secondary rhinaria as in the sexupara of *K. japonica* in structure, but secondary ones on the average more numerous in each segment in accordance with the antennae longer than in *K. japonica*. Antennal setae short and sparse, about 0.01 mm long on segment V; III with 0-3; IV with 0-3; V with 1-5 (usually 4); VI but processus terminalis with 1-3; processus terminalis usually with 5 stout ones, the apical one 0.01 mm long, but the basal one often indistict. Head ventrally with 12-19 setae on the furcate sclerite posterior to median ocellus. Rostrum very short, not reaching the middle of fore and middle coxae; ultimate rostral segment slightly spinulose, convex marginally, 0.066- 0.076 (0.071) mm long, 0.65-0.77 times as long as second segment of hind tarsus, with 7-10 setae. Femorotrochanter, in hind legs, slightly spinulose along the posterior margin, 0.72-0.78 (0.74) times tibial length; tarsus with transverse rows of spinules. First tarsal segment invariably with 1 pair of long setae and 1 shorter, spine-like seta. Empodial setae feeble, a little exceeding the points of claws. Dorsum without intersegmental bands of sclerites in abdomen. Cornicles usually present on the marginal position of abdominal tergite VI, not projecting, sclerotized narrowly round, each with a distinct rim round, surrounded by 0-2 setae, about 0.030 mm long in the longest diameter; sometimes one or both of the pair completely absent or reduced to small sclerites. Abdominal setae short and dorsally sparse, at most 0.020-0.035 mm long on tergite VIII. Setae on sternites more densely arranged in neatly single rows. Genital plate posteriorly arcuate, transverse, weakly pigmented all over, with 19-26 setae scattered over except for medio-anterior part. Dark pigmented, small sclerites present laterally to genital plate. Anal plate with 14-23 setae, of which 8-15 setae are present in the front. Cauda semicircular, with 4-9 setae. Fore wings with a simple media; the veins as in *K. nirecola*. Hind wings with 2 oblique veins. Biometric data shown in Table 6.

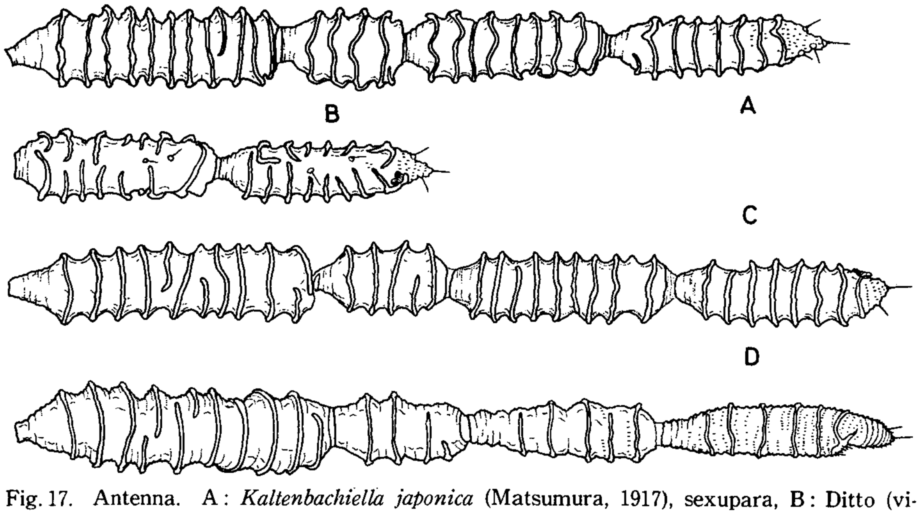

Fig. 17. Antenna. A: *Kaltenbachiella japonica* (Matsumura, 1917), sexupara, B: Ditto (viewed from the opposite side), C: *Kaltenbachiella spinosa* sp. nov., emigrant, D: *Kaltenbachiella nirecola* (Matsumure, 1917), emigrant.

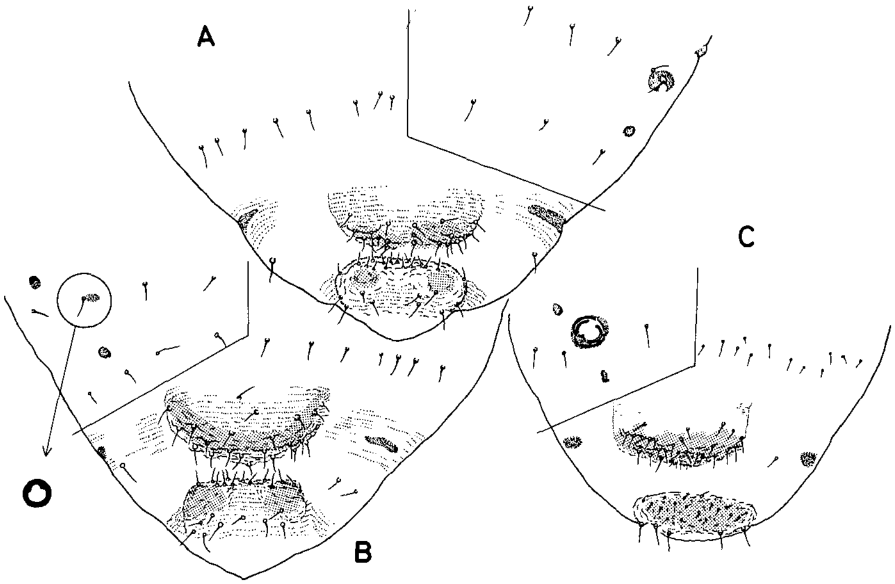

Fig. 18. Abdomen. A : *Kaltenbachiella spinosa* sp. nov., emigrant ; right, dorsum ; left, ventrum, B : *Kaltenbachiella japonica* (Matsumura, 1917), sexupara ; right, ventrum ; left, dorsum, C : *Kaltenbachiella nirecola* (Matsumura, 1917), emigrant ; right, ventrum ; left, dorsum.

Fundatrix adult (Fig. 24c). Antennae 4-segmented or 3-segmented with an incomplete slit, 0.09–0.12 times as long as body, 0.63–0.68 times hind femorotrochanter length ; wholly smooth. Other characters as in the fundatrix adult of *Kaltenbachiella japonica.* Biometric data shown in Table 24.

Gall (Plate IV B and C). As in *K. japonica*, but generally with larger spines arranged more roughly.

Specimens examined. Fundatrix adults, No. 1, Bibai, Hokkaidô, ex a gall on *Ulmus davidiana* var. *japonica*, 14-VII-1984 ; No. 2, Tsumagoi, Gumma Pref., ex a gall on *Ulmus*, 30-VII-1961 (Takahashi collection) ; No. 3 and 4, Bibai, Hokkaidô, ex galls, 11-VII-1984.

Emigrants, No. 1-8, Tsumagoi, Gumma Pref., ex a gall on *Ulmus*, 30-VII-1961 (Takahashi collection) ; No. 9-15 (No. 11 the holotype), Bibai, Hokkaidô, ex galls on *Ulmus davidiana* var. *japonica*, 14 and 15-VII-1984.

Emigrant progeny, No. 1-8, from the emigrant of No. 9 and 10.

Kaltenbachiella nirecola (Matsumura, 1917)

Gobaishia nirecola Matsumura, 1917, p. 76–78 [originally described].
Gobaishia nirecola : Matsumura, 1931, p. 1293 [briefly described and illustrated].
Gobaishia nirecola : Shinji, 1941, p. 1065.
Kaltenbachiella nirecola : Börner and Heinze, 1957, p. 294.
Kaltenbachiella nirecola : Higuchi and Miyazaki, 1969, p. 55 [host].
Colopha nirecola : Eastop and Hille Ris Lambers, 1976, p. 160.

Remarks. Bag-shaped velvet galls formed on the midrib are commonly found in

Bibai and Tôbetsu, central Hokkaidô, on *Ulmus davidiana* var. *japonica.* The antennal characteristics of this species almost correspond with the description of *Gobaishia nirecola* (Matsumura, 1917). However, although *nirecola* was described as having unbranched media in the fore wings, the specimens at hand show branched ones. Further Matsumura (1917) recorded a single elm leaf on which 12 galls of *nirecola* were formed. This situation is apparently of *Tetraneura* spp. In the original description of *nirecola* some characteristics of *Tetraneura* spp. seem to be mixed in proper ones of *nirecola.* I take the antennal characters in the original description for true diagnostic ones of *Kaltenbachiella nirecola.* The records of the secondary host given by Matsumura (1917) are much doubtful and probably of *Tetraneura* spp. Exules of *K. nirecola* were acquired by Dr. Miyazaki from the roots of *Polygonum orientale.*

First instar larva borne by the emigrant (Fig. 19). Body elongate, 0.461-0.472 mm long, 0.41-0.45 times as wide as long, not sclerotized except for legs, antennae, rostrum, head and clypeus, with distinct wax gland plates scattered over. Eyes present latero-ventrally, sclerotized, rather large, with 3 conspicuously prominent ommatidia. Antennae short, 4-segmented, 0.109-0.127 (0.117) mm long, 0.25-0.26 times as long as body, 0.96-1.09 (1.02) times hind femorotrochanter length. Antennal segments I and II smooth and cylindrical. Antennal segment III becoming thicker apically with broadly convex margins, uniformly sclerotized, with minute spinules scattered over apical half only. Antennal segment IV gradually becoming narrower with convex margins towards processus terminalis, which is roundly prominent; with minute spinules densely scattered all over, not imbricated, with a depression at the primary rhinarium. Primary rhinarium transverse, with an oval opening, from which 2 semitransparent tonguelets extend to both lateral sides like curved horns across the outer margin of antennae; surrounded by dense cilia in a single line. Antennal setae long and all acute. Antennal segment IV with 7 setae; the longest one present on processus terminalis rather subapically, 0.039-0.041 mm long. Antennal segment III with 4 setae arranged in the middle of the segment. Head

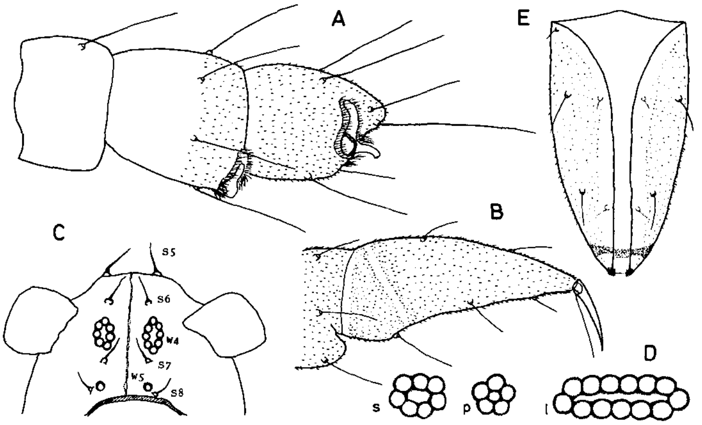

Fig. 19. *Kaltenbachiella nirecola* (Matsumura, 1917), first instar larva borne by the emigrant. A Antennal segments II-IV, B Hind tarsus, C Ventrum of head, D Abdominal wax gland plates; s-spinal plate, p-pleural plate, l-lateral plate, E Ultimate rostral segment.

weakly and broadly sclerotized on the dorsum and ventrum, with a median, unsclerotized line. Cephalic setae all acute and feeble; on the dorsum 1 pair (S1) outside medio-posterior wax plates, 1 pair (S2) anteriorly to latero-posterior wax plates, 1 pair (S3) just above antennal bases, 1 pair (S4) medio-anteriorly, and 1 pair (S5) rather medio-frontally; on the ventrum 2 pairs (S6, S7), anteriorly and posteriorly, to medio-anterior wax plates, and 1 pair (S8) outside small facial wax plates. Rostrum reaching hind coxae; segment II weakly sclerotized over apical half on the underside, rather finely spinulose along labial groove; ultimate segment convergent with broadly convex margins over all, finely spinulose except for labial groove, with 10 setae, 0.52-0.55 (0.54) times hind femorotrochanter length. Femorotrochanter almost smooth (very slightly with some spinules along the hind margin). Tibia densely with spinules which expand from the apex across the middle. Tarsus completely united, tapering with slightly convex margins dorsally, densely with minute spinules; claws almost straight; empodial setae simple and feeble, a little exceeding the points of claws. Dorsum not sclerotized, cauda and sternite VIII distinctly spinulose. Body setae all short and acute. Pronotum with 2 transverse rows of 1 spinal and 1 lateral pair of setae, anteriorly and posteriorly. Each of mesonotum and metanotum with 2 lateral pairs, anteriorly and posteriorly, and with 1 pleural pair and 1 spinal pair. Abdominal tergites I-VI with 1 spinal, 1 pleural and 1 lateral pair. Tergite VII with 1 spinal and lateral pair, and tergite VIII with only 1 spinal pair. Cauda with 1 pair of shorter setae. Abdominal sternites II-VII with 1 spinal pair of setae, and VIII with 4 setae. Spinal setae on tergite III 0.011-0.014 mm long and those on VIII 0.021-0.025 mm long. Wax gland plates black rimmed, waving in the outer margin, rather dimorphic between spinal-pleural position and lateral position: in the former central fields are almost circular, while in the latter transversely elongate as slits; central field black rimmed. Circumferential cells circular, partitioned from one another, a little darker than the central field, without conspicuously darker part. Head with 5 pairs of wax gland plates; their arrangement similar to that of the corresponding form of *Paracolopha morrisoni,* but on the ventrum W4s located posteriorly to S6s instead of S5s, being longitudinal. W5s reduced to 1 or 2 cells. Pronotum with 1 spinal and 1 lateal pair. Meso- and metanotum and abdominal tergites I-VI each with 1 spinal, 1 pleural and 1 lateral pair. Tergite VII with 1 spinal and 1 lateral pair; spinal wax plates exceptionally often larger than lateral ones. Tergite VIII with 1 pair of small spinal wax plates. Spiracles inconspicuous, without a distinct pore, not upheaving at all, not sclerotized. Biometric data shown in Table 15.

Emigrant adult (Fig. 17D and Fig. 18C). Body elongate oval, 1.35-1.72 (1.52) mm long, without wax gland plates. Antennae 6-segmented, but rarely 5-segmented with segment V completely fused with VI (No. 3), 0.55-0.61 (0.58) mm long, 0.35-0.42 (0.38) times as long as body, 0.92-1.03 (0.98) times as long as hind tibia, with segments V and VI long relatively to segment III. Antennal segment VI and the basal parts of IV and V showing slight imbrication; processus terminalis on VI intensively imbricated, being finely partitioned. Spinules present on whole segment VI and in a less degree on segment V, arranged neatly in transverse rows across interrhinarial parts; in No. 9 and No. 10 present additionally on segment IV and further rudimentarily on III. Antennal segment III relatively short, 0.54-0.64 (0.57) times combined length of IV, V and VI; IV marginally irregular, short, 0.41-0.47 times as wide as long except for the width of secondary rhinaria; V thicker to about basal 1/3, more apically largely rugged marginally, at subapical position 0.26-0.37 times as wide as long and on the average 1.9 times the width of the base; VI slender, narrower basally, with almost parallel margins, 0.21-0.25 times as wide as long, with developed, pointed processus terminalis, but in No. 9 and No. 10 with less developed one. Secondary rhinaria present on III-VI, very narrow, a little less than 0.0025 mm wide, sparsely arranged on IV, V and VI, highly projecting on segment III and in a much less degree on IV-VI, usually covering a little more than 1/2 the circumference on each segment from the ventral side, with a few shorter rhinaria out of the arrangment of others on each segment, not distinctly appearing as bright lines; the apical or subapical one on segment VI often thicker towards the primary rhinarium or rarely connected to the neighboring rhinarium. Primary rhinarium on segment V without an opening, not ciliated, joined with the apical secondary rhinarium; one on segment VI with a ciliated transverse opening, from which the apical or subapical secondary rhinarium issues, without a distinct projection from the opening, with a few ciliated circular accessory rhinaria. Antennal setae short and scarce, present mainly on the dorsal side, 0.015-0.020 mm long on segment V; III with 1-4 setae; IV usually without setae but rarely with 1-3 ones; V with 2-5 setae; VI but processus terminalis with 1-3 setae; processus terminalis with 4 thick setae at the apex and subbasally with 1 shorter one, the longest one of which is about 0.015 mm long. Head ventrally with 12-19 setae and setal sockets on the furcate sclerite posterior to median ocellus. Rostrum very short, a little exceeding fore coxae; ultimate rostral segment, slightly spinulose, convex laterally, 0.060-0.073 (0.068) mm long, 0.46-0.56 times as long as second segment of hind tarsus, with about 10 setae. Femorotrochanter, in hind legs, slightly spinulose along posterior margin, 0.69-0.77 (0.74) times tibial length; tarsus with transverse rows of minute spinules. First segment of tarsus with 1 pair of spine-like setae and 1 pair of feeble and longer setae in all legs. Empodial seta feeble, a little longer than claws. Abdominal tergites without sclerites. Cornicles present rather pleurally on abdominal tergite VI or at the level of the spiracles of tergite VI, hardly projecting, sclerotized narrowly round, each with a distinct rim round, usually surrounded by no setae, about 0.030 mm long in maximal length. Abdominal setae short and dorsally sparse, 0.020-0.025 mm long spinally on tergite III and 0.025-0.030 mm long spinally on tergite VIII. Setae on sternites more densely arranged in single rows. Genital plate posteriorly arcuate, transverse, dark pigmented posteriorly, with 24-33 setae, which are mainly distributed over the posterior half, partly expanding over the central field; additionally with several rudimentary setae represented only by setal sockets. Dark pigmented, small sclerites present laterally to genital plate. Anal plate not comprising lobes, rather dark pigmented, with 18-21 setae distributed almost evenly. Cauda semicircular, with 3-5 setae. Fore wings with once branched media, but sometimes with simple one in one of them; the veins conspicuously bordered, narrow. Hind wings with 2 oblique veins. Biometric data shown in Table 7.

Exule adult (Fig. 20). Body broadly rounded, 1.45-1.64 mm long and 0.74-0.78 times as wide as long; head and prothorax not elongated. Antennae, legs, rostrum and head rather strongly sclerotized. Distinctly rimmed, transverse wax gland plates scattered over. Eyes rather large, well sclerotized, with only 3 ommatidia. Antennae 5-segmented, not imbricated, 0.12-0.13 times body length, 0.61-0.65 times hind femorotrochanter length. Antennal segment III cylindrical, rudimentarily with a few spinules, 0.56-0.63 times as wide as long, always without a slit; segment IV short and broad, thicker apically with convex margins, subapically 0.86-0.88 times as wide as long, spinulose; segment V broad but thinner than IV, not tapering, with slightly convex margins when viewed from lateral, with broad processus terminalis, with dense cilia of primary rhinarium, with spinules in transverse rows, 0.52-0.59 times as wide as long. Primary rhinarium represented by an opening from which 1 frucate tonguelet projects, densely surrounded by long cilia; tonguelet on segment IV with short arms; that on segment V with long arms both extending to lateral sides. Antennal setae acute, rather long, on segment IV maximally 0.023-0.025 mm long and 0.64-0.72 times the width of the segment. Antennal segment III without setae; IV with 4 ones; V with 6-7 ones in addition to cilia. Head with 2 symmetric sclerites sperated by a rather broad, median belt. Cephalic setae rather long, about 0.04 mm long at maximum; their arrangement as in the emigrant progeny. Rostrum very short, not reaching middle coxae; ultimate segment convergent with slightly convex margins, slightly spinulose, with about 10 long setae, 0.23-0.26 times hind fomorotrochanter length. Femorotrochanter and tibia thinly with spinules along posterior margin; tarsus smooth. Femorotrochanter slender, 0.19 times as wide as long. Tarsus completely separated into 2 segments by an unsclerotized line in every leg; first tarsal segment with 1 pair of normal setae. Maximal value of width/length in fore, middle, and hind tarsus as follows: 0.45-0.50, 0.48-0.53, 0.40. Second tarsal segment marginally straight, more or less tapering in every leg. Setae on tibia and tarsus short, but stout. Claws normal, 0.36-0.45 times tarsal length in hind legs; empodial setae feeble and simple, a little shorter than claws. Body setae rather long, arranged in a row across each tergite; 0.028-0.046 mm long

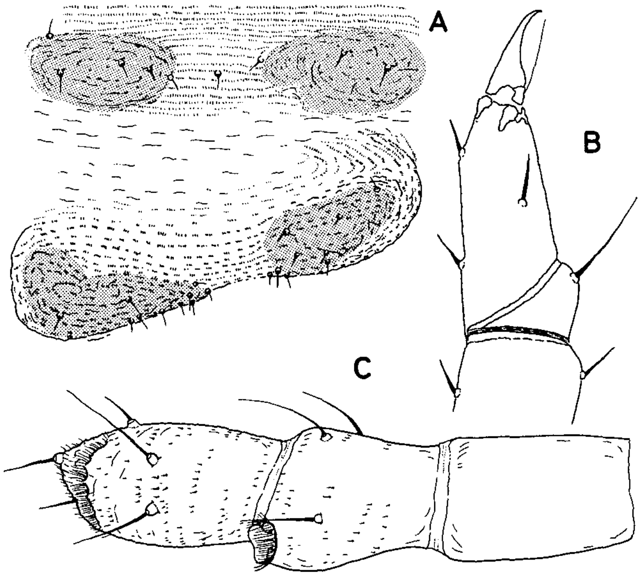

Fig. 20. *Kaltenbachiella nirecola* (Matsumura 1917), exule adult. A Genital and anal plates, B Fore tarsus, C Antennal segments III-V.

spinally on abdominal tergite III, and 0.041-0.046 on tergite VIII. Wax gland plate oval to strongly transverse, with regularly waving margin; comprising 1 central field and circumferential cells. Circumferential cells almost same-sized, circular, black rimmed marginally, and in large magnification another narrow rim visible inside outer rim. Central field strongly transverse and distorted in lateral rows, with the same brightness as cells. On head W3s transverse and W4s longitudinal, and the latter located below S6s instead of S5s. Spinal and lateral wax plates on abdominal tergite III 0.045-0.049 and 0.062-0.077 mm long, respectively, in maximal length. Arrangement of wax plates as in the emigrant progeny. Cornicles absent. Genital plate strongly transverse, posteriorly arcuate, laterally upheaving to form 2 dark sclerotized lobes, wholly with 9-11 setae; long anterior setae absent. Dark sclerotized plates present laterally to genital plate. Anal plate conspicuously prominent, also with 2 dark sclerotized lobes, on which 13-21 setae are present; gonochaetae absent. Cauda with 3 setae. Biometric data shown in Table 20.

Fundatrix adult (Fig. 24D; Fig. 25A). Body broadly rounded, without clearly bordered wax gland plates. In margins head continuous to rounded body. Legs short, almost hidden under the body in dorsal view. Antennae 4-segmented, 0.10-0.11 times body length, 0.60-0.68 times hind femorotrochanter length; segment III longest, roundish marginally at apex and base, narrower in the middle, apically with primary rhinarium; segment IV broadly rounded, at apex with ciliated primary rhinarium, which is not long projecting. Antennae slightly spinulose only in segment IV. Femorotrochanter spinulose only along posterior margin. Tibia spinulose in apical half. Tarsus smooth, 1-segmented or with a rudimentary slit at dorso-basal position. Rostrum short, not reaching to the middle of fore coxae and hind ones; ultimate segment straightly converging with a wide angle. Spiracle plates small and indistinct. Appendages rather strongly pigmented. Biometric data shown in Table 25.

Gall (Plate IV D and E). Projecting upwards from the midrib, oblong, rather bag-shaped, with some protuberances on the apical half, often pressed narrowly, with the apex broadly rounded, narrower to the base but not becoming petiole-like, often reddish in the apical half, otherwise in green but paler than the leaf, densely with short and white hairs, rather thin in the wall.

Specimens examined. Fundatrix adults, No. 1-3, Bibai, Hokkaidô, ex 3 galls on *Ulmus davidiana* var. *japonica*, 9～13-VII-1981 (Y.Yamaguchi leg.).

Emigrant adults, No. 1-4 (No. 4 the neotype), Nopporo (near Sapporo), ex a gall on *Ulmus davidiana* var. *japonica*, 30-VII-1983; No. 5-8, Bibai, ex a gall, 13-VII-1981 (Y.Yamaguchi leg.); No. 9 and 10, Tsumagoi, Gumma Pref., ex a gall, 25-VII-1960 (Takahashi collection).

Emigrant progeny, No. 1-8, from the emigrants of No. 5-8.

Exule adults, No. 1-3, Nopporo (near Sapporo), ex *Polygonum orientale* (root), 16-IX-1982 (M. Miyazaki leg.).

Kaltenbachiella elsholtriae (Shinji, 1936)

Astegopteryx ? sp. Monzen, 1929, p, 20 〔recorded from Morioka, Sendai and Tôkyo〕.
Eriosoma elsholtriae Shinji, 1936, p. 13-14 〔originally described〕.
Gobaishia japonica : Mordvilko, 1935, p. 116-118 〔recorded from Vladivostok〕.

Eriosoma elsholtriae : Higuchi and Miyazaki, 1969, p. 55 [host plant].
Kaltenbachiella elsholtriae : Eastop and Hille Ris Lambers, 1976, p. 232.
Kaltenbachiella elsholtriae : Ghosh, 1981 [redescribed from Japanese specimens].

Remarks. The biology of the present species is not clarified. In autumn the leaf-curling galls of this species are never rare on the secondary host, *Elsholtzia ciliata*, in the campus of Hokkaidô University. Although sexuparae having sexuales in the abdomen appear abundantly on the leaf-curlings in the season, the corresponding galls of this species have not been discovered on the possible primary host *Ulmus davidiana* var. *japonica*. It is impossible for the exule adults or larvae to hibernate on the secondary host because *Elsholtzia ciliata* is an annual plant and withers utterly in autumn. It is no doubt that *K. elsholtriae* passes a holocyclic life cycle including host alternation, the sexuparae migrating to some unknown plant other than *Ulmus davidiana* var. *japonica*. Leaf-curlings are formed at Sapporo in early to mid August by first instar larvae not of the fundatrix but of the exule-form. Therefore, the larvae are undoubtedly borne by emigrants although they have not been collected so far.

The present species has often been erroneously regarded as the exule generations of *K. japonica* (Mordvilko, 1935, p. 117-119 ; Shinji, 1941), but the characteristics of wax gland plates and the karyotype (Akimoto, unpublished) clearly distinguish *K. elsholtriae* from *K. japonica* or *K. spinosa* as a good species. I have often been informed that leaf-curlings of the present species were found on *Elsholtzia ciliata* in localities practically without *Ulmus davidiana* var. *japonica*, e.g. Kyôto and Saitama Pref.

First instar larva borne by the emigrant (Fig. 21). Three skins of the first instar larva were found by dissecting early galls on *Elsholtzia ciliata*. The following description based on these skins.

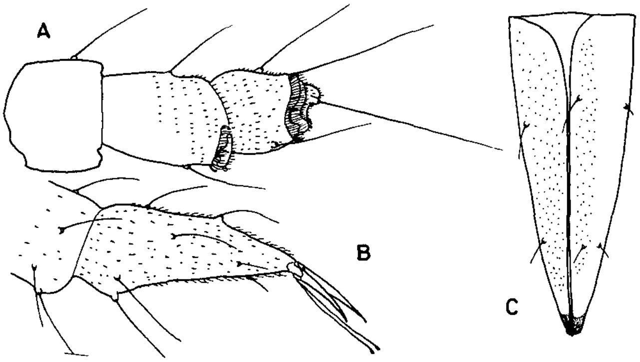

Fig. 21. *Kaltenbachiella elsholtriae* (Shinji, 1936), first instar larva borne by the emigrant. A Antennal segments II-IV, B Hind tarsus, C Ultimate rostral segment.

Antennae 4-segmented, 0.091-0.096 mm long, 0.95-1.0 times hind femorotrochanter length. Antennal segment III thicker apically with broadly convex margins, coarsely with spinules over apical half ; segment IV roundish marginally, with processus terminalis roundly prominent, spinulose. Primary rhinarium as in the corresponding form of *Kaltenbachiella nirecola*. Antennal segment IV with 7 setae ;

the longest one present on processus terminalis rather subapically, somewhat blunt at apex, 0.046 mm long. Segment III with 4 setae on apical half only. Ultimate rostral segment convergent with almost straight margins, spinulose, with 10 setae, 0.79 times hind femorotrochanter length. Femur with rudimentary spinules; tibia, except for basal part, coarsely spinulose. Tarsus completely united, tapering with almost straight margins, densely with stout spinules; claws almost straight; empodial setae spatulate apically, about 1.5 times claw length. Wax gland plates as in the exule adult in structure. Biometric data shown in Table 15.

Exule adult (Figs. 22 and 23). Body broadly rounded, 1.13-1.37 mm long and 0.69- 0.79 times as wide as long, membranous except for antennae, legs, rostrum and head, which are all weakly sclerotized; head and prothorax not elongated. Distinct wax gland plates scattered over. Eyes with only 3 ommatidia. Antennae 4- or 5-segmented, not imbricated, 0.10-0.13 times body length, 0.60- 0.69 times hind femorotrochanter length; when 4-segmented, segment III thicker apically with conspicuously arcuate posterior margin, at the apex about 0.6 times as wide as long, slightly spinulose in apical half, when 5-segmented, this segment divided as the middle; apical segment tapering to slender processus terminalis, with slightly convex margins, slightly spinulose, at base 0.55-0.58 times as wide as long. Primary rhinarium represented by an opening from which 1 tonguelet projects, ciliated; the segment next to the apical one with 1 furcate small tonguelet; the apical segment with 1 tanguelet extending apically, additionally with a few accessory rhinaria. Antennal setae short; segment III, in apical half, with 4 setae (in 5-segmented antennae they present only on segment IV), which are 0.005-0.01 mm long; apical segment with 1-2 setae basally and 5 ones apically in addition to cilia. Head almost wholly weakly sclerotized, without a median slit. Cephalic setae short, about 0.02 mm long at maximum; their arrangement almost as in the emigrant progeny of *Kaltenbachiella spinosa* exule. Rostrum reaching middle coxae or a little exceeding them; ultimate segment convergent with almost straight margins, spinulose, with 9-10 short setae, 0.39-0.41 times hind femorotrochanter length. Femorotrochanter slightly spinulose in posterior half; tibia rudimentarily spinulose. Femorotrochanter rather broad, 0.28-0.31 times as wide as long. Tarsus with an incomplete oblique slit on dorso-basal position in every leg. Fore tarsus parallel or slightly diverging marginally in basal half and suddenly tapering in apical half, with 1 enlarged seta at ventro-middle point; middle and hind tarsus somewhat inflated on ventro-basal part, but there with normal setae, tapering with straight margins more apically. Maximal value of width/length in fore, middle and hind tarsus as follows: 0.63-0.80, 0.59-0.75, 0.57-0.61. Setae on tibia and tarsus short. Claws straight

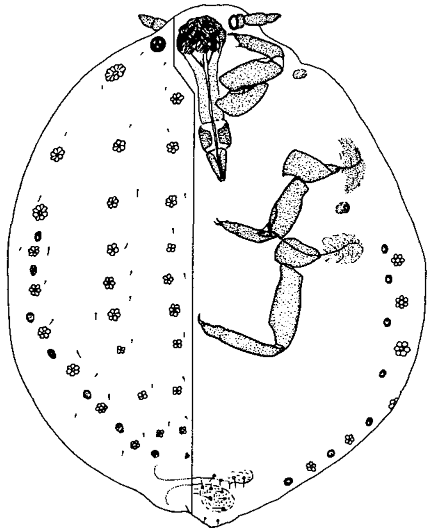

Fig. 22. *Kaltenbachiella elsholtriae* (Shinji, 1936), exule adult. Right: Ventrum; Left: Dorsum.

except for apical part, 0.47–0.51 times tarsal length in hind legs; empodial setae feeble, simple, shorter than claws. Body setae simple; in maximal length 0.025–0.030 mm long spinally on abominal tergite III, and 0.020 mm long on tergite VIII. Wax gland plate rather petal-shaped, comprising 1 circular central field and circular circumferential cells, not transversely extended near to posterior end. Circumferential cells same-sized, dark rimmed and further innerly with a border line, inside granulated and darker than central field. Head with 5 pairs of wax plates; their arrangement as in the corresponding form of *Kaltenbachiella spinosa*, and W4s located just posteriorly to S5s; W5s (facial wax gland plates) reduced to 2 or 3 cells without a central field. Pronotum with 1 spinal and 1 lateral pair; the latter exceptionally longitudinal. Meso- and metanotum and abdominal tergites I–VI each with 1 spinal, 1 pleural and 1 lateral pair. Tergite VII with or without 1 spinal pair ; if any, central field absent. Tergite VIII without wax gland plates. Spinal and lateral wax plates on abdominal tergite III 0.029–0.030 and 0.030–0.035 mm long, respectively, in maximal length. Genital plate not sclerotized, transverse, posteriorly arcuate, laterally upheaving to form 2 lobes, wholly with 8–9 setae; anterior setae absent. Lateral dark plates absent. Anal plate with 2 unpigmented, slightly upheaving lobes, with 10–13 setae; gonochaetae absent. Cauda with 2 setae. Biometric data shown in Table 21.

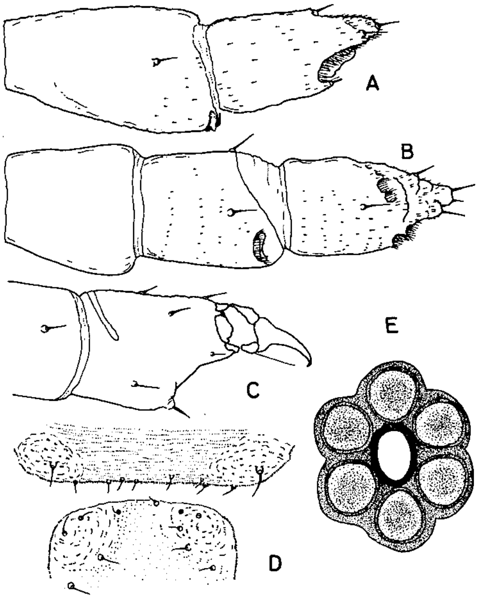

Fig. 23. *Kaltenbachiella elsholtriae* (Shinji, 1936), exule adult. A Antennal segments III-IV (in 4-segmented antenna), B Antennal segments III-V (in 5-segmented antenna), C Fore tarsus, D Genital and anal plates, E Abdominal wax gland plate.

Sexupara adult (Fig. 7D). Body elongate oval, 1.37–1.68 (1.57) mm long, without wax gland plates. Antennae 6-segmented, 0.49–0.57 (0.54) mm long, 0.32–0.37 (0.34) times as long as body, 0.89–1.02 (0.95) times as long as hind tibia. Antennal segment III longer than the combination of segments V and VI, and 0.85–1.05 times as long as IV, V and VI combined. Antennal segment IV always shorter then V; segment V as long as or a little shorter than VI. Antennal segment III smooth; IV with a few spinules; V and VI markedly spinulose and showing imbrication. The spinules arranged densely as transverse lines on segment VI but more sparsely and irregularly on V. Antennal segment V always thicker towards the apex, and VI slender, almost parallel marginally, on apical 1/3 gently converging to processus terminalis, which is projecting short and narrowly. Secondary rhinaria present on segments III–VI, narrow, 0.003–0.004 mm wide on III, sparsely arranged on V and VI, highly projecting on III and IV and in a much less degree on V and VI, usually covering a little more than 1/2 the circumeference on each segment from the ventral side, with a few much shorter rhinaria out of the arrangement of others on each segment. The basal secondary rhinarium on segment III usually conspicuously broad, inside with a few spots. Primary rhinarium on segment V without an opening, not ciliated, joined with the apical secondary one; that on segment VI without a distinct opening and distinct cilia, joined with the apical secondary rhinaria, which stretches half round the segment, with a few ciliated semicircular accessory rhinaria. Antennal setae short and sparse, 0.015-0.020 mm long on segment V; III with 0-3 setae; IV with 1 seta or without one; V with 3-4 setae; VI but processus terminalis with 1-2 setae on apical half; processus terminalis with 4 thick setae, the apical one of which is longest and thickest. Head ventrally with 6-10 setae on the furcate sclerite posterior to median ocellus. Rostrum short, not reaching to the middle of fore coxae and hind ones; ultimate segment spinulose, 0.086-0.106 (0.099) mm long, 0.71-0.88 times as long as second segment of hind tarsus. Femorotrochanter thinly with spinules, 0.70-0.78 (0.73) times tibial length; tarsus densely with transverse rows of stout spinules. First segment of tarsus also spinulose, with 1 spine-like seta and 1 pair of feeble and longer setae in all legs. Empodial seta longer than claws, at apex slightly capitate. Abdominal tergites without sclerites. Cornicle absent. Abdominal setae short and dorsally sparse, 0.020-0.025 mm long on the spinal position of each of tergites III and VIII. Setae on sternites more densely arranged in single rows. Genital plate posteriorly arcuate, with transverse rows of denticles, comprising 2 weakly sclerotized lobes, which are indistinct and often look like a single plate, altogether with 33-45 setae on the lobes and on the space posterior to them, without a distinctly sclerotized plate on each lateral side. Anal plate weakly pigmented, rather showing reticulation, slightly forming 2 lobes, altogether with 9-12 setae. Cauda rather triangular-like, with 2-5 setae. Fore wings with simple media; the veins conspicuously bordered, narrow. Hind wings with 2 oblique veins. Biometric data shown in Table 8.

Gall. Exules are found covered with much waxy secretion within small hollows formed on intercostal regions. One leaf usually has several hollows. The leaf is intensively wrinkled and distorted around the hollows, turning reddish purple along the midrib.

Specimens examined. Exule adults, No. 1 (neotype) and 2, Sapporo, ex *Elsholtzia ciliata* (leaf gall), 6-IX-1983; No. 3, Mt. Hakkôda (Tsuta-onsen), Aomori Pref., ex *Elsholtzia ciliata* (leaf gall), 8-VIII-1984.

Emigrant progeny, No. 1-3, skins taken from early leaf galls, Mt. Hakkôda, Aomori Pref., ex *Elsholtzia ciliata*, 8-VIII-1984.

Sexuparae, No. 1-7, Sapporo, ex *Elsholtzia ciliata* (leaf gall), 22-IX-1984; No. 8-11, Sapporo, ex *Elsholtzia ciliata* (leaf gall), 3-X-1984.

Kaltenbachiella glabra, sp. nov.

Remarks. Galls of this species were collected in Taiwan by Dr. S. Aoki from *Ulmus uyematsui*, which is endemic to the island's mountain region above an altitude of 2000 m. The galls were globular, without petiole, occurring on the midrib of leaves. Skins of the fundatrix first instar larva were obtained from the galls. This stage is very similar to the corresponding stage of *Kaltenbachiella japonica* in the membranous body with fragmentary sclerites on the thorax, conspicuously large spiracle pores and very short appendages compared with *Paracolopha*, etc. As shown in Table 10, the first instar larva of *K. glabra* differs from that of *K. japonica* in the longer hind femur, longer ultimate rostral segment, larger spiracle pores and larger tibia/femur ratio.

The galls collected were of early stages and contained fundatrix adults mostly previous to birth. The present species is distinguishable from other *Kaltenbachiella* species by the characters of the gall and fundatrix. The gall is rather similar in appearance to that of the Japanese *Kaltenbachiella nirecola*, but is readily distinguishable by the completely smooth surface (densely short-hairy in *K. nirecola*). The fundatrix adult of *K. glabra* is distinguished from that of *K. nirecola, K. japonica*, or *K. spinosa* in its wide sclerotization on the head and in its tarsi separated completely into two segments.

The phylogenetic relationships of *Ulmus uyematsui*, the primary host plant, within the genus *Ulmus* is at present uncertain (Bate-Smith and Richens, 1973). From this elm species *Eriosoma lishanense* and *Tetraneura yezoensis* have been recorded so far (Akimoto, 1983). *Kaltenbachiella*, the *Eriosoma ulmi* group and *Tetraneura* are the groups which are firmly associated with the section *Ulmus* as the primary hosts (group F and G of Bate-Smith and Richens). The parasite composition on *Ulmus uyematsui* may show that this elm is a component of the section *Ulmus*. Probably in some Quaternary time, the elements of the section *Ulmus* may have migrated southwards from the middle latitudes of East Asia and invaded into Taiwan through the Taiwan Strait which is supposed to have then become land (Tokuda, 1969). Subsequently, following the recovery of warmer climates and the resultant appearance of the Taiwan Strait, the ancestor of *U. uyematsui*, together with its parasites, may have survived as relict only in the island's mountain region. In the continent of East Asia, after the glacial ages the section *Ulmus* retracted the range northwards, and at present the elements are distributed to the north of 32°N. L. (Horikawa, 1976).

Fundatrix first instar larva (skin). Head widely sclerotized; thoracic dorsum fragmentarily sclerotized; abdominal dorsum membranous. Antennae 4-segmented, almost as in the corresponding form of *K. japonica*; antennal segment IV with 7 setae, of which the longest one is simple and about 0.05 mm long. Ultimate rostral segment longer than in the corresponding form of *K. japonica*, almost straightly converging, 0.75-0.76 times hind femorotrochanter length. Tibia thicker to the apex, 0.95 times as long as femorotrochanter in hind legs, with stouter and more numerous setae than in *K. japonica*. Spiracle pores conspicuously large, 0.015-0.020 mm long in maximal diameter. Dorso-apical setae on tarsus long and capitate at apex, 0.04 mm long in hind legs. Chaetotaxy on body as in *K. japonica*. Biometric data shown in Table 11.

Fundatrix adult (Fig. 24E and Fig. 25B). Body broadly rounded, without clearly bordered wax gland plates. In margins head continuous to rounded body. Legs short, almost hidden under the body in dorsal view. Antennae 4-segmented, 0.17-0.25 times body length, 0.52-0.58 times hind femorotrochanter length: segment III slightly convex marginally, thicker towards the apex, smooth, apically with primary rhinarium; segment IV rather rectangular or oblong, with some denticles, apically with primary rhinarium, which is not long-projecting and more thinly ciliated than in *K. nirecola*. Head widely sclerotized, with large, unsclerotized spaces surrounding antennal bases. Coxae spinulose; femorotrochanter smooth or with rudimentary spinules along posterior margin; tibia and tarsus smooth. Tarsus distinctly divided into 2 segments; second segment tapering. Rostrum short, exceeding the middle of fore coxae and middle ones; ultimate segment very slightly convex marginally, converging with a wide angle. Spiracle plates rather small. Genital plate strongly transverse, not clearly defined, weakly sclerotized at 2 points but not forming lobes, with 17-23 setae. Anal plate weakly sclerotized, with 20-25 setae. Progeny of the fundatrix with 6 longitudinal rows of wax gland plates, which are consisting of same-sized circular cells and lack central fields. Intercellular spaces black pigmented. Biometric data shown in Table 26.

Gall (Plate IV F). Projecting upwards from the midrib, almost globular with roundish apex, weakly inflating at a few points in the apical half, smooth on the surface, without hairs, with thick wall. The midrib not bending down at the point on which the gall occurs.

Specimens examined. Fundatrix adults, No. 1-4 (No. 4 the holotype), near Wushe (about 2000 m alt.), Nantou county, Taiwan, ex 4 galls on *Ulmus uyematsui*, 7-V-1984 (S. Aoki leg.).

Fundatrix first instar larvae, No. 1 from the gall of No. 1 adult; No. 2 from the gall of No. 2 adult; No. 3 from the gall of No. 4 adult.

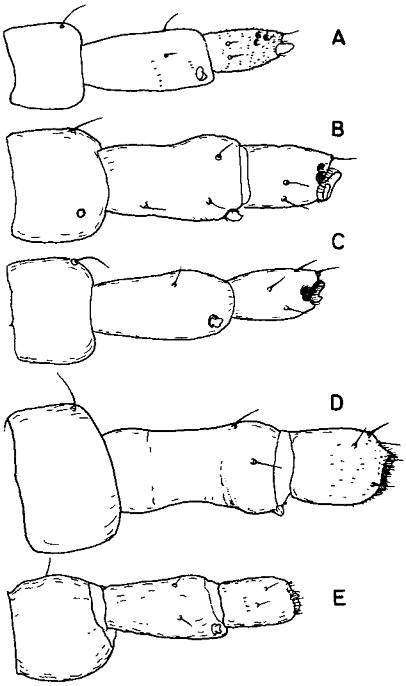

Fig. 24. Antenna of fundatrix adult. A: *Paracolopha morrisoni* (Baker, 1919), B: *Kaltenbachiella japonica* (Matsumura, 1917), C: *Kaltenbachiella spinosa* sp. nov., D: *Kaltenbachiella nirecola* (Matsumura, 1917), E: *Kaltenbachiella glabra* sp. nov.

KEY TO THE EAST ASIAN SPECIES OF THE TETRANEURINI EXCEPT TETRANEURA

Alate

1. Fore wing with once branched media. Hind wing with 2 oblique veins. 2
— Fore wing with simple media. Hind wing with 1 or 2 oblique veins. 3
2. Antennal segments V and VI, when combined, much shorter than III. Segment IV almost as long as V, and segment VI shorter than V. Antennae wholly smooth. Cornicle absent. Secondary rhinaria ring-like, not upheaving. On the aerial parts of *Carex*. .... *Colopha kansugei* (alate exule or sexupara)
— Antennal segments V and VI, when combined, much longer than III. Segment IV much shorter than V, and segment VI longer than V. Antennal segment VI spinulose. Cornicles present as pores with the circumferences narrowly sclerotized. Secondary rhinaria very narrow, linearly covering antennal segments, highly upheaving on segment III. From bag-shaped gall on *Ulmus davidiana* var. *japonica*. ....*Kaltenbachiella nirecola* (emigrant)
3. Hind wings with 1 oblique vein. Antennal segments IV, V and VI subequal in length. Fore

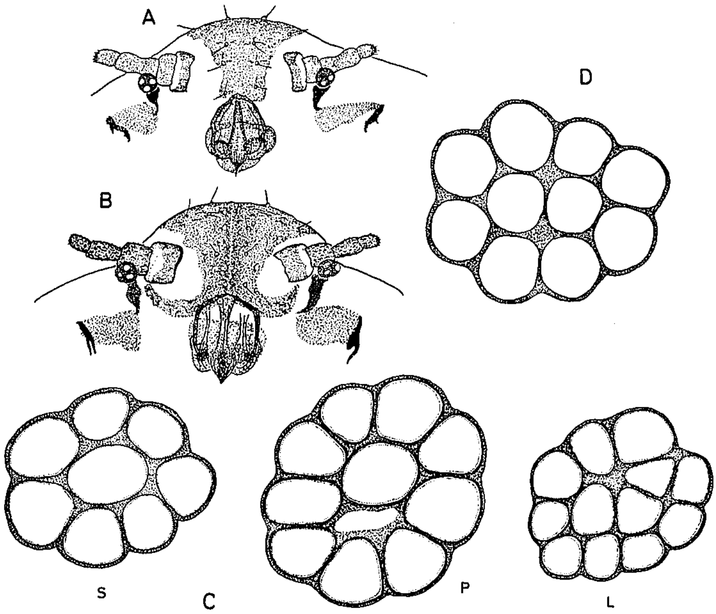

Fig. 25. A : *Kaltenbachiella nirecola* (Matsumura, 1917), fundatrix, ventrum of head, B : *Kaltenbachiella glabra* sp. nov., fundatrix, ventrum of head, C : *Kaltenbachiella nirecola* (Matsumura, 1917), wax gland plates of 4th instar larva occurring in the gall, D : *Kaltenbachiella glabra* sp. nov., wax gland plate of 1st instar larva occurring in the gall.

wings shaded in brown. Veins of wings rather broad and pale. Secondary rhinaria not upheaving. 4

— Hind wings with 2 oblique veins. Antennal segment V much longer than IV, and segment VI longer than or almost as long as V. Fore wings almost transparent. Veins of wings narrow and dark. Secondary rhinaria highly upheaving. 5

4. Cornicle absent. From petiolate-globular gall on *Zelkova serrata* ....*Paracolopha morrisoni* (emigrant)

— Cornicle present on the pleural position. On the roots of small bamboos or on the trunk of *Zelkova serrata*. ....*Paracolopha morrisoni* (sexupara)

5. Antennal segments V and VI, when combined, shorter than III. From hollow gall on *Elsholtzia ciliata*. ....*Kaltenbachiella elsholtriae* (sexupara)

— Antennal segments V and VI, when combined, much longer than III. 6

6. With sexuales in the abdomen. From globular, spiny gall on *Ulmus davidiana* var. *japonica*. ....*Kaltenbachiella japonica* (sexupara)

— With embryos of the exule-form in the abdomen. From globular, spiny gall on *Ulmus davidiana* var. *japonica*. ....*Kaltenbachiella spinosa* sp. nov. (emigrant)

Exule adult

1. Cornicles present. Abdominal tergites V, VI and VII each with 4 wax gland plates.... 2

— Cornicles absent. Abdominal tergites V and VI each with 6 wax gland plates, and tergite VII with 4. 3

2. Tarsi separated into 2 segments. Claws normal. On *Carex*. ......*Paracolopha takahashii*

— Tarsi 1-segmented. Claws long and stout. On the roots of small bamboos. ....*Paracolopha morrisoni*

3. Body oblong, tapering posteriorly. Tarsi 1-segmented. Fore tarsi thickened, ventro-

anteriorly with a well developed setal socket. The point of the socket exceeding the base of claws. On the aerial parts of *Carex*. .... *Colopha kansugei*

— Body broadly rounded. Tarsi separated into 2 segments or with an incomplete, oblique slit. 4

4. Fore tarsi 2-segmented, with normal setae on the first segment. Lateral wax gland plates strongly extended. On the roots of *Polygonum orientale*. .... *Kaltenbachiella nirecola*

— Fore tarsi imperfectly segmented with the first segment thickened and prominent, with 1 seta in the ventro-anterior position. Lateral wax gland plates not extended transversely. From hollow gall on *Elsholtzia ciliate*. .... *Kaltenbachiella elsholtriae*

DISCUSSION

Phytogeographers have long noticed a close floral resemblance between East Asia and eastern North America (e.g. Gray, 1846; Li, 1952; Hara, 1962; Van Steenis, 1962), and the origin of this resemblance has been attributed to an ancient common flora called Arcto-Tertiary flora. Most genera originated from this flora are at present distributed disruptively over the two regions and consist mainly of broad-leaved deciduous trees. Fossil records have repeatedly shown that in early Tertiary time the ancestral elements had continuous and extensive distributions from Eurasia to North America through the Bering Land Bridge over high latitudes (e.g. Leopold, 1969 and see Hotta, 1974; Pielou, 1979). However, upon the late Eocene or early Oligocene the climates were radically deteriorated, and the resultant migration of the boreo-subtropical flora towards low latitudes had caused floral disruption at least by the middle Miocene and finally created disjunctive distributional patterns limited to the warm-temperate region in each of the two continents (Wolfe, 1978; Matthews, 1980). The common genera of Arcto-Tertiary origin are thus supposed to have preserved morphological uniformity at the generic level in both continents over about 10 and some million years at least since the middle Miocene. Moreover, there are some grass species which are distributed in Japan and southeastern North America and show no remarkable differences in morphology (Koyama and Kawano, 1964). Little has been, however, discussed about biogeographical patterns of insect taxa from the standpoint of long-lasting evolutionary stasis. I believe that the species of the Eriosomatinae, which are associated with elements from the Arcto-Tertiary flora, are suitable material for this problem. In the following lines the origin and history of the tetraneurine genera are considered in connection with the distributional transitions of the host plants.

Stasis at the generic level

The genus *Colopha* includes two holocyclic and one anholocyclic species, and the holocyclic species are exclusively associated with elms of the section *Blepharocarpus*. This section, consisting of *Ulmus laevis* and *U. americana*, is rather broadly distributed in each of south-central Europe and eastern North America, harbouring the holocyclic species different between the continents (Fig. 26B). This disjunctive distributional pattern suggests the past extensive range through high latitudes of Europe, Asia and North America. In the Beringia tropical climates in the middle Eocene were replaced by temperate ones in the late Oligocene, and during this interval the plant genera that currently have close species pairs between the two continents could expand their distributions across the Beringia (Wolfe, 1978;

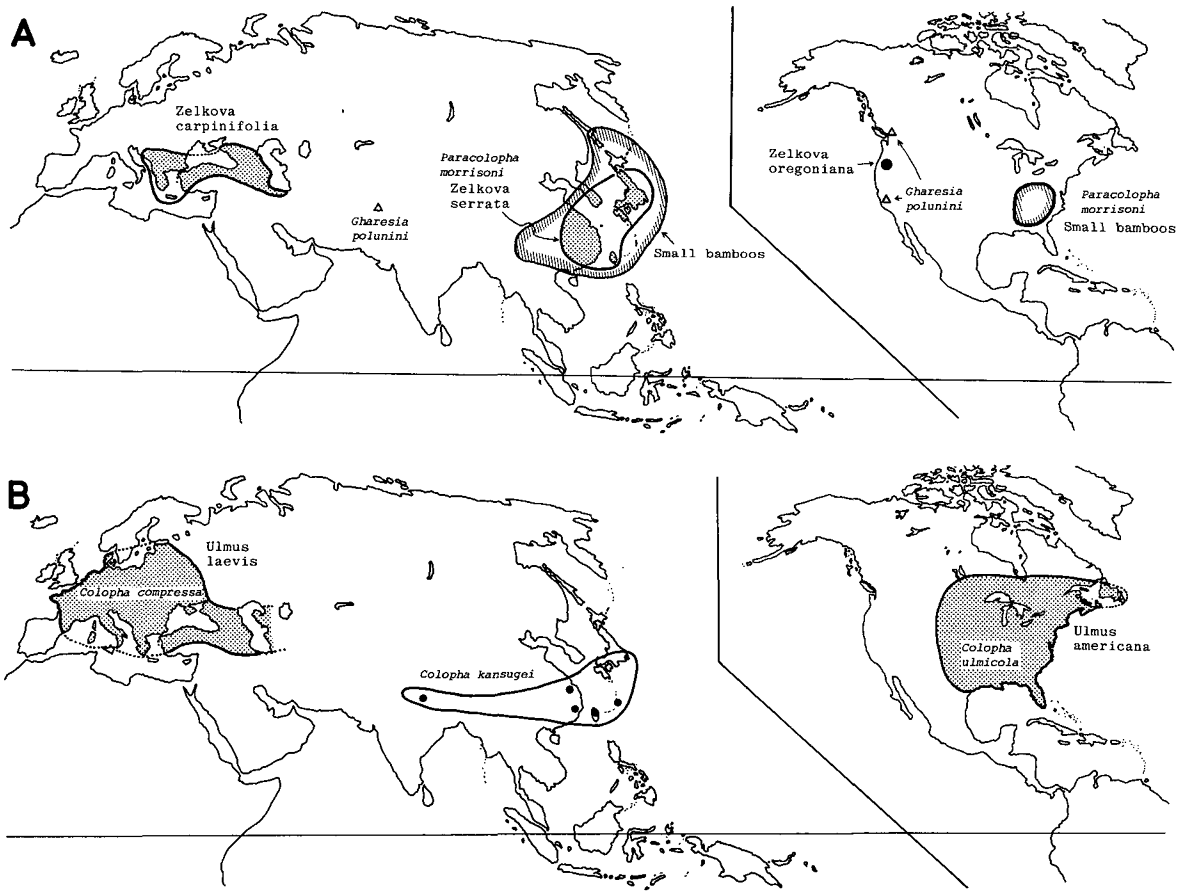

Fig. 26.A. Approximate distributions of *Zelkova* and small bamboos. The genus *Zelkova* is distributed in Transcaucasia-southern Europe (*Z. carpinifolia*) and in East Asia (*Z. serrata*). A fossil species, *Z. oregoniana,* is known from the west coast of North America. Small bamboos include *Arundinaria, Sasa, Pleioblastus* and *Sasamorpha* in East Asia, but only *Arundinaria* in eastern North America. Holocyclic populations of *Paracolopha morrisoni* are found in almost all the range of *Zelkova serrata.* There are anholocyclic populations of *P. morrisoni* on small bamboos in America. *Gharesia polunini* is found in the Himalayan region and the west coastal region of North America. *Zelkova* is absent at present in these regions, but was present at least in the west coastal North America.

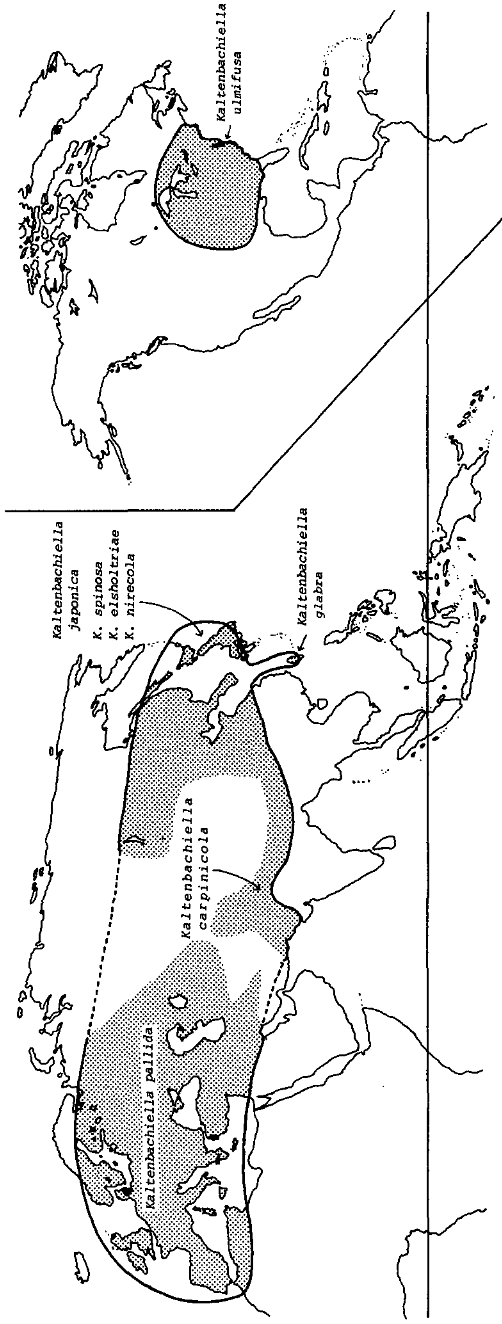

Fig. 27. Approximate distribution of the section *Ulmus* of the genus *Ulmus*. The distributions of the *Kaltenbachiella* species are superimposed on those of the section *Ulmus*. *K. carpinicola*, however, is reported to have been collected from galls occurring on *Carpinus* sp. in northern India (Ghosh, 1981). There is no record of *Kaltenbachiella* in China yet.

←

Fig. 26.B. Approximate distribution of the section *Blepharocarpus* of *Ulmus*. *Colopha compressa* and *Colopha ulmicola* are holocyclic and widely distributed within the ranges of *Ulmus laevis* and *U. americana*, respectively. *Colopha kansugei* is obligatorily anholocyclic on the secondary host, and distributed in Japan widely, west to southern China and Nepal.

Matthews, 1980). In the early Miocene, however, cooler climates were introduced over middle and high latitudes (Tanai, 1972), and then, despite a temporary recovery of warmer climates in the middle Miocene (Matthews, 1980), the Beringia was covered with boreal hardwood and conifer forests (Wolfe and Tanai, 1980). Since that time, further deteriorated climatic conditions have absolutely prevented the reestablishment of warm-temperate forests around the Beringia (see Pielou, 1979 ; Matthews, 1980). Throughout the period when the Arcto-Tertiary elements could migrate across the Beringia, the climates became consistently deteriorated (Tanai, 1972), and in accordance with this climatic trend, the flora of the Beringia changed its components from tropical and evergreen to temperate and deciduous ones. The plants directly derived from tropical elements, such as some genera of the Magnoliaceae, are currently restricted to warm and moist areas of Southeast Asia and America. The time when the section *Blepharocarpus* of the genus *Ulmus* originated and expanded over high latitudes may correspond with some time when temperate climates became dominant there, probably with some Oligocene time. This section is more or less cool-tolerant and could enter into considerably boreal realms especially in Europe.

The present distribution of the section may also be explained by supposing the existence of a North Atlantic land bridge as invoked by Richards (1965) for some aphids. The supposed one, once stretching from Europe through Greenland to North America, was finally separated as late as the Eocene, 49 million years ago (Pielou, 1979). The time of separation is apparently too early to explain the distribution of the section, because the North Atlanctic region was in tropical climates at that time. Moreover, this line of assumption cannot reasonably explain the occurrence of *Colopha kansugei* in East Asia. At least for the Eriosomatinae North Atlantic land bridges may have no significance as a pathway between Eurasia and North America.

The aphids of *Colopha* undoubtedly expanded in association with their primary hosts over the high latitudes of Europe, Asia and North America previous to the Miocene. East Asia is supposed to have been one of the refuges for warm-temperate woody elements during the Ice Age (Haffer, 1982). However, for some reason, elms of the section *Blepharocarpus* must have been eliminated from East Asia and have left an associated *Colopha* species, *C. kansugei*, on the secondary host as permanent parthenogenetic populations. These asexual populations may have been derived from facultatively parthenogenetic strains which previously accompanied the holocyclic populations. In East Asia, in fact, some species of *Ulmus* became extinct. Although it is difficult to distinguish the section *Blepharocarpus* from the section *Ulmus* in fossils, there is possibility that among the 11 fossil *Ulmus* species recorded from Japan *U. appendiculata* is a member of the former section. This species, which is characterized by large leaves and their strongly asymmetric base, is most similar in general characters to the fossil species *U. speciosa*, which is common among the Miocene geoflora of western North America (Tanai, 1961, p. 316-321). *U. speciosa* coincides in these characters with *U. americana* rather than with the other extant American species of *Ulmus*. Moreover, Tanai pointed out that *U. appendiculata* closely resembles *U. americana* as well as *U. davidiana* (of the section *Ulmus*) occurring in China.

Colopha kansugei, ranging from southwestern Japan through the Ryûkyû

Islands, Taiwan, southern continental China to the eastern Himalaya, agrees in distributional pattern with warm-temperate plant species or species groups called the Sino-Japanese elements (Kanai, 1963). Concerning herbaceous plants, Hara (1972) pointed out that the same species or species groups distributed in the Sino-Japanese region often have another range disjunctively in eastern North America, and concluded that such species or species groups must have been in evolutionary stasis for at least 5 million years. On the basis of the recent paleobotanical knowledge the duration of such stasis should be more than twice as much. The similarity between such plants and *Colopha* in distribution again points to the probability that *Colopha* originated before the Miocene.

The time of origin in Kaltenbachiella and Tetraneura

The aphids of *Kaltenbachiella* and *Tetraneura* are associated with elms of the section *Ulmus* (*Ulmus* F and G groups of Bate-Smith and Richens, 1973). As shown in Fig. 27, the extant components of this section surpass other elms in the temperate Eurasia, having extensive and continuous ranges up to 67°N.L. to the north (Uehara, 1961) and entering into more or less arid climatic conditions (e.g. Pakistan and Afghanistan) (Elias, 1970 ; Bate-Smith and Richens, 1973). In North America this section is represented only by *U. rubra*, which occupies almost the same realm as *U. americana*. The origin of the section, therefore, must have been prior to the break of floral exchanges in the Bering Land Bridge, that is prior to the late Miocene. It is, however, no doubt that the section achieved successful adaptation to a world-wide progress of cool and arid climates especially after the Oligocene, having expanded its range into the boreal region. Tanai (1972), on the basis of fossil records, showed that in the Miocene new component species appeared luxuriantly in the Arcto-Tertiary genera *Acer, Fagus* and *Carpinus* under deteriorating climatic conditions, and pointed out that a parallel substitution of new components occurred also in the Ulmaceae. I therefore postulate that the genus *Kaltenbachiella* derived in this time from the stock of *Colopha* in association with the section *Ulmus* which was rapidly diverging and expanding the range. In fact, the extant species of *Kaltenbachiella* are, at least in East Asia, all distributed more northwards than *Colopha kansugei* and *Paracolopha morrisoni*. *Kaltenbachiella* thus must have migrated through the Beringia in a much later and more cool-conditioned time than when *Colopha* did, probably in the earliest Miocene.

There is good reason to believe that the genus *Tetraneura* derived most recently among the genera of the tribe Tetraneurini. First, it is restricted to the Palearctic region (Hille Ris Lambers, 1970), suggesting that its origin is not traceable back to the time before the middle Miocene. A few species of *Tetraneura* (*T. akinire* and *T. ulmi*) occur in North America ; they were introduced from Europe together with the primary hosts and have persisted in the new territory at least for about 100 years, but exclusively on the European elm, without colonizing native elms (Monell, 1882 ; Patch, 1910 ; Palmer, 1952 ; Hille Ris Lambers, 1970 ; Knowlton, 1983). Moreover, in northeastern Asia *Tetraneura* is currently the most prospering genus among the Eriosomatinae not only in the number of species but also in the population density. If the genus had only appeared before the section *Ulmus* was distributed over the Beringia, there would have been no ecological and climatic conditions to prevent it from entering into North America. In addition, there is paleoclimatological evidence that gramineous grasses, the secondary hosts of *Tetraneura*, advanced luxuriant divergence and expanded extensively after the Pliocene (Axelrod, 1948). All ecological and distributional aspects of the genus thus consistently point to its origin in the late Miocene to the Quaternary and in Eurasia. While *Colopha* was persisting in generic stasis in East Asia, Europe and North America, *Tetraneura* must have derived from the Eurasian stock of *Colopha* (Akimoto, in preparation) and radiated rapidly.

The time of origin in Paracolopha

There is high possibility that the natural range of the genus *Paracolopha* is restricted to East Asia. If this view is true it can be thought that *Paracolopha* derived from a species of *Colopha* in East Asia after the temperate flora was eliminated from the Beringia. The genus *Colopha*, the supposed ancestral taxon of *Paracolopha*, have persisted in morphological stasis at the generic level even after *Paracolopha* branched off.

There is another possibility of the origin of *Paracolopha*, however. *Zelkova*, the primary host of *P. morrisoni*, has disjunctive ranges in East and West Asia (Fig. 26A). The secondary hosts, small bamboos, are distributed in East Asia, especially in Japan with abundant species diverging, and in southeastern North America with two species each having a close counterpart in Japan (Nakai, 1934). Although North America is out of the current natural range of *Zelkova*, there is fossil evidence that this plant taxon had lasted there from the early Tertiary until the Miocene (Chaney, 1959 ; Niklas, 1977). Therefore, if *Paracolopha* was of sufficiently early origin, it may be possible that the genus invaded North America together with *Zelkova* and small bamboos. In that case, as in the case of *Colopha kansugei*, the possibility cannot be ruled out that parthenogenetic populations have persisted on small bamboos after the extinction of *Zelkova*. In this connection, it is very interesting to know if there is any valid method (electrophoretic or cytological analysis) to test the possible nativeness of the North American populations of *P. morrisoni*.

Stasis at the specific level

In connection with evolutionary stasis an eriosomatine, *Gharesia polunini*, deserves to be mentioned. So far as based on the wax gland structure it does not belong to the Tetraneurini but to another phylogenetic stock, which has diverged on *Zelkova*. The alate form, however, shows no essential difference from that of *Colopha*. In any case, the fact that there is no definite clue for its relationships to other eriosomatine genera may mean that it is quite in primitive state.

Gharesia polunini is distantly disrupted in distribution into the western Himalayas and the west coastal region of North America (Stroyan, 1963 ; Hille Ris Lambers, 1966 ; Foottit and Mackauer, 1980) (Fig. 26A). In these regions, where no species of *Ulmus* or *Zelkova* natively occur, it passes an anholocyclic life on the aerial parts of *Carex*, the secondary host. It is difficult to imagine any human agency which might have once been concerned with the current pattern of distribution of this aphid. Whether *G. polunini* is, for the primary host, associated with *Zelkova* or *Ulmus* (of the section *Blepharocarpus*), it is very probable that in the past some of their elements existed in these regions as part of their continuous and extensive ranges, as perceived from Fig. 26A and B. In fact, in the coastal region of North America *Zelkova* and *Ulmus* are known from the sediments of the Oligocene to the Miocene (Niklas, 1977; Giannasi and Niklas, 1977). In the Himalayan region, further, the distribution of the eriosomatine genus *Hemipodaphis* corroborates the possibility of *Zelkova* having once existed there. *H. monstrosa*, an anholocyclic species in the secondary host, is known from Darjeeling, northern India, while *H. persimilis* and the closely related species, "*Colopha*" *caucasica*, are associated with *Zelkova* respectively in Japan and Caucasia (Dzhibladze, 1960; Akimoto, 1983). Thus, *Gharesia polunini* can be thought to have been holocyclic with host alternation between some ulmaceous tree and *Carex* in both regions in the past.

I am very much inclined to believe, therefore, that *Gharesia polunini* has been in morphological stasis at the specific level for 10 and some million years at least since the middle Miocene. Another possibility is that the parthenogenetic populations migrated across the Beringia in association with *Carex* in, say, the Quaternary. This possibility is, however, powerless in explaining why *Gharesia polunini* is much restricted in distribution in spite of the abundance of *Carex* all over the world.

Through my comparative studies of the eriosomatine life cycles I (1983) postulated that the Tetraneurini derived from some archaic forms living in clustering leaf-rolls. It is the opinion here adopted that the ancestral groups, unless they are extinct, must, in general, have persisted with their morphologies and life cycles basically unchanged, as discussed in the instances above. I maintained that the ancestral form of the Tetraneurini can be sought in the genera *Hemipodaphis* and *Aphidounguis* and that the time of origin of these genera can be approached to the earliest Tertiary or the latest Cretaceous when the host plant genera evolved rapidly. These aphid genera are called "ancestral" in the sense that other extant Eriosomatinae have passed, in some Tertiary time, through the same adaptive zone as occupied by the genera and that these genera have continued to stay in the same adaptive zone ever since. They are associated with warm-temperate plants as the primary hosts, and these plants are now restricted to separate regions, surviving as relicts. The supposed enormously old origin does not seem exceptional in the genera of the Aphidoidea. Richards (1965) also considered that, in the Callaphidini, *Myzocallis, Tuberculatus* and *Tinocallis*, which are associated with Arcto-Tertiary elements, had become established by the end of the Cretaceous.

In conclusion, I would like to emphasize that, if the supposed long evolutionary stasis is general, the concept of ancestor-descendant relationship is very useful and quite important in constructing phylogeny and studying evolution instead of being an obstruction (Nelson and Platnick, 1984) to systematics and biogeography.

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TABLES

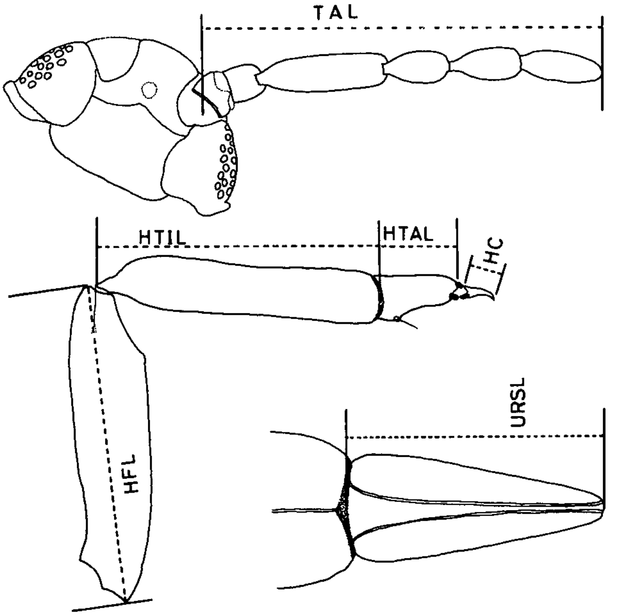


Fig. 28. Measurement. TAL-Total antennal length, URSL -Length of ultimate rostral segment, HFL-Length of hind femorotrochanter, HTIL-Length of hind tibia, HTAL-Length of hind tarsus, HC-Hind claw length.

Table 1. Interspecific comparisons of galls and fundatrix first instar larvae.

	Aphidounguis mali	*Kaltenbachiella japonica*	*Paracolopha morrisoni*	*Tetraneura yezoensis*	*Tetraneura sorini*
Gall	leaf-roll (clustering type)	globular on midrib	globular with petiole on intercostal part	slender pouch-like with petiole on intercostal part	pouch-like with petiole on intercostal part
Extent of sclerotization on dorsum	with oval sclerites arranged in 6 longitudinal rows	with fragmentary sclerites mainly on thorax	wholly weakly sclerotized	wholly sclerotized	wholly strongly sclerotized
Body length (mean) sample size, in mm.	0.57-0.68 (0.62) 6	0.41-0.46 (0.44) 10	0.52-0.60 (0.55) 10	0.57-0.60 (0.61) 14	0.80-1.00 (0.90) 16

Table 2. Biometric data for *Paracolopha morrisoni* emigrant.

Number	BL	TAL	A III	A IV	A V	A VI	HFL	HTIL	HTAL	URSL	S III	S IV	S V	S VI	RLA
1-1	2.03	0.46	0.171	0.073	0.076	0.081	0.422	0.566	0.124	0.095	10	5	6	5	100 : 43 : 44 : 47
1-2	2.36	0.52	0.189	0.081	0.081	0.086	0.475	0.651	0.136	0.096	13	6	5	3	100 : 43 : 43 : 45
2-1	1.35	0.39	0.121	0.066	0.066	0.076	0.341	0.455	0.111	—	7	4	3	4	100 : 54 : 54 : 63
2-2	1.38	0.44	0.149	0.076	0.076	0.081	0.354	0.470	0.121	0.090	—	—	—	—	100 : 51 : 51 : 54
2-3	1.54	0.40	0.116	0.066	0.071	0.081	0.351	0.485	0.111	0.085	8	5	4	3	100 : 57 : 61 : 70
2-4	1.76	0.46	0.232		0.076	0.088	0.414	0.550	0.116	0.086	15		4	4	
3-1	2.30	0.53	0.202	0.073	0.081	0.091	0.463	0.626	0.131	0.107	15	4	5	4	100 : 36 : 40 : 45
3-2	2.12	0.48	0.174	0.073	0.076	0.078	0.434	0.576	0.126	0.105	13	5	6	3	100 : 42 : 43 : 45
3-3	2.10	0.48	0.171	0.073	0.078	0.080	0.434	0.586	0.121	0.102	11	5	5	3	100 : 43 : 46 : 46
3-4	2.18	0.47	0.169	0.076	0.071	0.076	0.434	0.596	0.131	0.101	12	4	5	4	100 : 45 : 42 : 45
3-5	2.12	0.48	0.194	0.071	0.073	0.083	0.444	0.616	0.131	0.106	16	4	5	3	100 : 36 : 38 : 43
TZ*	2.1	0.53	0.19				0.36	0.58			12-15	4	5-8	5-7	100 : 38 : 48 : 47

Measurements in mm. BL-Body length. TAL-Total antennal length. A III-VI-Length of antennal segments III-VI. HFL-Length of hind femorotrochanter. HTIL-Length of hind tibia. HTAL-Length of hind tarsus. URSL-Length of ultimate rostral segment. S III-VI-Number of secondary rhinaria on segments II-VI. RLA-Relative length of antennal segments (III : IV : V : VI). TZ*-*Tetraneura zelkovisucta* from China. Same for other tables.

Table 3. Biometric data for *Paracolopha morrisoni* sexupara.

Number	BL	TAL	A III	A IV	A V	A VI	HFL	HTIL	HTAL	URSL	S III	S IV	S V	S VI
1	1.82	0.57	0.227	0.076	0.91	0.106	0.49	0.68	0.141	0.136	16	5	4	5
2	—	0.58	0.229	0.086	0.083	0.096	0.49	0.67	0.136	0.131	14	6	4	4
3	1.86	0.60	0.247	0.078	0.091	0.106	0.58	0.74	0.146	0.151	15	4	5	4
4	2.21	0.68	0.272	0.091	0.096	0.123	0.61	0.88	0.166	0.171	17	5	4	5
5	1.81	0.55	0.197	0.078	0.083	0.104	0.50	0.66	0.136	0.157	11	4	4	3
6	1.63	0.59	0.227	0.091	0.086	0.111	0.51	0.72	0.141	—	17	5	6	4
7	1.73	0.48	0.178	0.071	0.071	0.086	0.47	0.61	0.121	0.123	10	4	4	3
8	1.69	0.52	0.237	0.076	0.081	0.087	0.50	0.64	0.131	0.146	19	4	6	4
OD*			?	0.08	0.096	0.08					12-15	5	6	5

OD*-Original description by Baker (1919).

Table 4. Biometric data for *Colopha kansugei* sexupara (S) and alate exule (A).

Number	BL	TAL	A III	A IV	A V	A VI	HFL	HTIL	HTAL	URSL	S III	S IV	S V	S VI
S-1	1.60	0.54	0.252	0.076	0.071	0.066	0.38	0.44	0.088	0.060	12	4	3	3
2	1.65	0.53	0.242	0.088	0.066	0.055	0.37	0.44	0.091	0.060	11	5	3	1
3	1.64	0.47	0.232	0.066	0.071	0.060	0.34	0.40	0.081	0.060	11	4	2	1
4	—	0.47	0.232	0.071	0.055	0.055	0.36	0.42	0.086	0.064	12	2	2	1
5	—	0.45	0.204	0.081	0.053	0.055	0.30	0.35	0.076	0.055	9	3	2	?
A-1	1.46	0.49	0.242	0.081	0.066	0.045	0.34	0.35	0.083	0.060	12	4	4	2
2	1.70	0.56	0.277	0.076	0.076	0.053	0.38	0.39	0.086	0.066	14	4	3	2
3	1.49	0.47	0.217	0.081	0.066	0.045	0.31	0.33	0.076	0.060	12	5	3	2
4	1.50	0.55	0.272	0.090	0.073	0.050	0.35	0.38	0.080	0.060	14	5	3	2
5	1.70	0.57	0.287	0.081	0.076	0.055	0.37	0.39	0.086	0.060	16	4	3	2
OD*	1.5	0.5									10	4	3	2
CG*	1.48	0.65	(70 :	18-20 :	18 :	15)		0.46	0.095		15-20 (18)	3-5	3-5	0-2

OD*-Original description by Uye (1924). CG*-*Colopha graminis* described by Takahashi (1937) from Taiwan.

Table 5. Biometric data for *Kaltenbachiella japonica* sexupara.

Number	BL	TAL	A III	A IV	A V	A VI	HFL	HTIL	HTAL	URSL	S III	S IV	S V	S VI	C
1	1.47	0.48	0.146	0.055	0.091	0.121	0.39	0.51	0.106	0.081	11	3	5	6	− −
2	1.65	0.54	0.222		0.101	0.126	0.39	0.51	0.116	0.086	19		7	7	− −
3	1.63	0.54	0.146	0.071	0.116	0.131	0.39	0.49	0.116	0.076	12	4	7	7	± −
4	—	0.51	0.146	0.066	0.086	0.116	0.36	0.48	0.116	0.086	12	6	7	6	− −
5	1.52	0.48	0.202		0.086	0.121	0.37	0.47	0.111	0.081	16		6	7	± −
6	1.53	0.49	0.146	0.060	0.081	0.116	0.38	0.49	0.111	0.081	13	4	5	7	− −
7	1.53	0.51	0.131	0.066	0.101	0.126	0.39	0.51	0.111	0.076	9	4	8	8	− ±
8	1.50	0.52	0.141	0.055	0.106	0.131	0.40	0.52	0.111	0.076	9	3	7	9	± ?
9	1.63	0.57	0.151	0.073	0.113	0.136	0.40	0.52	0.116	0.073	11	5	8	8	+ +
10	1.72	0.54	0.149	0.071	0.111	0.123	0.39	0.51	0.111	0.076	12	5	9	8	− +
11	1.57	0.55	0.146	0.081	0.108	0.131	0.39	0.52	0.121	0.076	11	7	7	8	− −
12	1.42	0.47	0.136	0.055	0.106	0.116	0.35	0.46	0.101	0.076	12	3	7	6	± −
13	1.39	0.51	0.146	0.060	0.096	0.116	0.36	0.46	0.106	0.071	13	3	7	8	± −
14	—	0.49	0.131	0.066	0.086	0.121	0.35	0.47	0.106	0.076	11	5	7	8	− −

C-Cornicle : + present, − absent, ± rudimentarily present.

Table 6. Biometric data for *Kaltenbachiella spinosa* emigrant.

Number	BL	TAL	A III	A IV	A V	A VI	HFL	HTIL	HTAL	URSL	S III	S IV	S V	S VI	C
1	1.31	0.52	0.156	0.071	0.116	0.109	0.31	0.41	0.106	0.069	13	5	12	6	? ?
2	1.36	0.57	0.171	0.076	0.111	0.116	0.33	0.44	0.106	0.076	15	6	10	8	− −
3	1.28	0.55	0.171	0.071	0.106	0.116	0.32	0.43	0.106	0.071	15	5	10	8	+ −
4	1.30	0.53	0.161	0.066	0.116	0.116	0.32	0.41	0.106	0.071	15	4	9	8	+ +
5	1.20	0.53	0.156	0.071	0.106	0.116	0.31	0.41	0.106	0.071	15	5	9	8	± +
6	1.33	0.55	0.176	0.060	0.106	0.121	0.33	0.44	0.106	0.076	15	4	8	9	+ ±
7	1.21	0.53	0.156	0.066	0.106	0.121	0.31	0.40	0.101	0.069	13	5	8	8	+ +
8	1.27	0.54	0.166	0.066	0.106	0.126	0.32	0.42	0.106	0.071	14	5	8	10	+ +
9	1.40	0.62	0.179	0.081	0.139	0.126	0.33	0.45	0.106	0.076	13	5	10	9	± ±
10	1.33	0.61	0.186	0.076	0.129	0.126	0.32	0.44	0.108	0.076	16	5	11	9	± ±
11	1.40	0.63	0.192	0.081	0.146	0.139	0.33	0.45	0.108	0.076	17	5	11	10	± ±
12	1.34	0.62	0.184	0.086	0.139	0.139	0.34	0.47	0.106	0.076	16	6	10	10	± ±
13	1.07	0.47	0.136	0.068	0.101	0.111	0.26	0.36	0.088	0.066	11	5	8	8	− −
14	1.03	0.49	0.141	0.060	0.101	0.112	0.26	0.35	0.088	0.066	12	4	8	7	− −
15	1.00	0.44	0.123	0.058	0.096	0.108	0.25	0.35	0.088	0.066	11	4	8	7	− −

Table 7. Biometric data for *Kaltenbachiella nirecola* emigrant.

Number	BL	TAL	A III	A IV	A V	A VI	HFL	HTIL	HTAL	URSL	S III	S IV	S V	S VI
1	1.35	0.57	0.176	0.076	0.106	0.134	0.41	0.57	0.131	0.060	12	4	5	6
2	1.42	0.56	0.171	0.076	0.106	0.131	0.40	0.59	0.131	0.063	11	4	5	4
3	1.55	0.56	0.176	0.076	0.101	0.121	0.43	0.61	0.136	0.066	10	3	4	4
4	1.53	0.55	0.174	0.076	0.103	0.121	0.42	0.59	0.136	0.071	10	3	4	4
5	1.57	0.61	0.176	0.076	0.116	0.141	0.45	0.59	0.141	0.071	11	2	6	5
6	1.45	0.59	0.176	0.076	0.108	0.141	0.44	0.59	0.141	0.071	12	3	6	4
7	1.45	0.61	0.184	0.081	0.111	0.146	0.45	0.60	0.141	0.071	12	4	5	6
8	1.52	0.59	0.179	0.071	0.108	0.151	0.45	0.59	0.141	0.066	9	3	4	5
9	1.61	0.58	0.186	0.076	0.101	0.123	0.43	0.59	0.131	0.073	13	2	6	6
10	1.72	0.60	0.197	0.086	0.096	0.126	0.46	0.61	0.136	0.073	12	4	5	5

Table 8. Biometric data for *Kaltenbachiella elsholtriae* sexupara.

Number	BL	TAL	A III	A IV	A V	A VI	HFL	HTIL	HTAL	URSL	S III	S IV	S V	S VI
1	1.68	0.54	0.219	0.066	0.083	0.091	0.44	0.57	0.121	0.096	13	3	5	2
2	1.52	0.54	0.232	0.063	0.078	0.081	0.40	0.57	0.121	0.106	14	2	3	2
3	1.64	0.55	0.227	0.070	0.092	0.090	0.42	0.59	0.126	0.101	13	3	5	2
4	1.67	0.54	0.207	0.073	0.086	0.085	0.44	0.59	0.126	—	15	4	4	2
5	1.66	0.57	0.232	0.078	0.081	0.098	0.44	0.59	0.129	0.106	18	4	3	3
6	1.60	0.55	0.219	0.068	0.081	0.091	0.41	0.59	0.131	—	13	4	3	3
7	1.53	0.56	0.229	0.078	0.091	0.086	0.43	0.60	0.128	0.103	13	4	5	2
8	1.45	0.49	0.207	0.063	0.076	0.076	0.38	0.55	0.118	0.101	14	3	3	3
9	1.62	0.56	0.227	0.063	0.086	0.105	0.39	0.55	0.118	0.091	14	3	4	4
10	1.37	0.51	0.212	0.058	0.085	0.087	0.38	0.53	0.111	—	15	2	4	3
11	1.54	0.55	0.217	0.071	0.081	0.092	0.40	0.55	0.121	0.086	13	4	3	3

Table 9. Biometric data for *Paracolopha morrisoni* fundatrix first instar larva.

Number	BL	HFL	HTIL	HTAL	TAL	BW	URSL	ASL	DSL	ESL	BS III	BS VII
1	0.581	0.127	0.106	0.043	0.099	0.238	0.091	0.061	0.053	0.025	0.010	0.043
2	0.556	0.132	0.122	0.046	0.106	0.259	0.096	—	0.051	0.030	0.008	0.033
3	0.581	0.132	0.112	0.046	0.114	0.264	0.091	0.061	0.051	0.025	0.010	0.033
4	0.597	0.134	0.122	0.046	0.112	0.264	0.091	0.064	0.058	0.030	—	0.031
5	0.523	0.129	0.110	0.046	0.109	0.246	0.086	0.060	0.051	0.030	0.008	0.035
6	0.532	0.127	0.112	0.046	0.101	0.243	0.086	0.056	0.051	0.028	0.006	0.030
7	0.525	0.122	0.106	0.041	0.101	0.233	0.086	0.056	0.048	0.028	0.006	0.030
8	0.532	0.128	0.109	0.046	0.112	0.259	0.086	—	0.051	0.028	0.010	0.031
9	0.528	0.119	0.106	0.043	0.101	0.248	0.084	0.051	0.048	0.026	—	0.025
10	0.547	0.129	0.112	0.046	0.112	0.269	0.086	0.051	0.051	0.030	—	0.031

Measurements in mm. BW-Body width. ASL-Length of the apical seta on antennal segment IV. DSL-Length of dorso-apical seta on hind tarsus. ESL-Length of empodial seta on hind tarsus. BS III-Length of spinal seta on abdominal tergite III. BS VII-Length of spinal seta on abdominal tergite VII. Same for other tables.

Table 10. Biometric data for *Kaltenbachiella japonica* fundatrix first instar larva.

Number	BL	HFL	HTIL	HTAL	TAL	BW	URSL	ASL	DSL	BS III	BS VII
1	0.446	0.086	0.071	0.030	0.063	0.208	0.061	0.048	0.035	0.005	0.007
2	0.436	0.091	0.076	0.030	—	0.213	0.063	0.046	0.033	0.006	0.008
3	0.461	0.086	0.071	0.033	0.066	0.203	0.061	0.048	0.033	0.008	0.008
4	0.451	0.086	0.071	0.033	0.066	0.203	0.061	0.051	0.035	0.009	0.009
5	0.411	0.081	0.066	0.030	0.066	0.203	0.061	0.046	0.035	0.008	0.008
6	0.449	0.081	0.068	0.030	0.068	0.208	0.061	—	—	0.008	0.009
7	0.426	0.086	0.068	0.033	0.076	0.203	0.061	0.046	0.035	0.005	0.010
8	0.441	0.091	0.071	0.033	—	0.203	0.061	0.051	0.035	0.009	0.010
9	0.454	0.086	0.071	0.030	0.061	0.203	0.061	0.048	—	0.006	0.008
10	0.416	0.086	0.071	0.030	—	0.193	0.061	0.046	0.033	0.008	0.010

Table 11. Biometric data for *Kaltenbachiella glabra* fundatrix first instar larva.

Number	HFL	HTIL	HTAL	URSL
1	0.098	0.093	0.035	0.073
2	0.101	0.096	0.035	0.076
3	0.101	—	—	0.076

Table 12. Biometric data for *Paracolopha morrisoni*, first instar larva borne by the emigrant.

Number	BL	BW	HFL	HTIL	HTAL	TAL	URSL	ASL	BW/BL	TAL/BL	TAL/HFL	URSL/HFL
1	0.482	0.198	0.112	0.083	0.041	0.096	0.096	0.041	0.411	0.200	0.864	0.864
2	0.436	0.183	0.106	0.081	0.041	0.099	0.096	0.035	0.419	0.227	0.929	0.905
3	0.446	—	0.112	0.081	0.041	0.096	0.096	0.035	—	0.216	0.864	0.864
4	0.461	0.190	0.106	0.081	0.041	0.096	0.094	0.041	0.412	0.209	0.905	0.881
5	0.464	0.203	0.112	0.081	0.043	0.101	0.093	0.041	0.437	0.219	0.909	0.832
6	0.446	0.193	0.106	0.079	0.041	0.101	0.095	0.041	0.432	0.227	0.952	0.890
7	0.444	0.203	0.112	0.083	0.043	0.096	0.096	0.041	0.457	0.217	0.864	0.864
8	0.441	—	0.109	0.081	0.043	0.096	0.096	—	—	0.218	0.884	0.884
9	0.456	0.203	0.112	0.081	0.043	0.101	0.096	0.039	0.444	0.222	0.909	0.864
10	0.456	0.198	0.112	0.081	0.044	0.095	0.096	0.041	0.433	0.208	0.850	0.864

Table 13. Biometric data for *Colopha kansugei* exule first instar larva.

Number	BL	BW	HFL	HTIL	HTAL	TAL	URSL	ASL	BW/BL	TAL/BL	TAL/HFL	URSL/HFL
1	0.737	0.307	0.112	0.095	0.041	0.119	0.051	0.030	0.416	0.163	1.068	0.459
2	0.674	0.274	0.108	0.094	0.041	0.132	0.051	0.030	0.407	0.197	1.221	0.469
3	0.704	0.278	0.112	0.100	0.041	0.129	0.054	0.033	0.396	0.185	1.154	0.484
4	0.612	0.239	0.106	0.093	—	0.127	0.055	0.033	0.390	0.208	1.196	0.517
5	0.578	0.245	0.105	0.094	—	0.112	0.056	0.035	0.423	0.194	1.063	0.531
6	0.620	0.236	0.106	0.091	—	0.114	0.052	0.032	0.380	0.185	1.077	0.493
7	0.724	0.291	0.109	0.095	0.041	0.117	0.056	0.034	0.401	0.162	1.070	0.512
8	0.612	0.255	0.127	0.106	0.046	0.142	0.056	0.035	0.417	0.233	1.116	0.438
9	0.643	0.255	0.122	0.101	0.043	0.132	0.058	0.036	0.397	0.206	1.083	0.479
10	0.612	0.245	0.123	0.101	0.046	0.136	0.056	0.035	0.400	0.223	1.103	0.453
11	0.627	0.245	0.124	0.102	0.045	0.133	0.056	0.035	0.390	0.214	1.073	0.449
12	0.649	0.235	0.112	0.098	0.042	0.130	0.056	0.037	0.362	0.202	1.168	0.500
13	0.612	0.239	0.114	0.095	0.041	0.127	0.053	0.032	0.390	0.208	1.111	0.467

Table 14. Biometric data for *Kaltenbachiella spinosa*, first instar larva borne by the emigrant.

Number	BL	BW	HFL	HTIL	HTAL	TAL	URSL	ASL	BW/BL	TAL/BL	TAL/HFL	URSL/HFL
1	0.406	0.198	0.101	0.084	0.046	0.119	0.063	0.043	0.488	0.294	1.175	0.625
2	0.393	0.177	0.099	0.086	0.043	0.113	0.065	—	0.452	0.286	1.138	0.656
3	0.401	0.177	0.101	0.082	0.046	0.121	0.065	0.046	0.443	0.301	1.190	0.640
4	0.441	0.203	0.101	0.086	0.046	0.117	0.066	0.046	0.460	0.264	1.150	0.650
5	0.415	0.183	0.101	0.081	0.043	0.115	0.065	0.045	0.440	0.276	1.130	0.645
6	—	—	0.096	0.083	0.045	—	0.064	0.045	—	—	—	0.663
7	0.406	0.198	0.101	0.076	0.043	—	0.062	0.045	0.488	—	—	0.615
8	0.395	0.193	0.101	0.085	0.043	0.112	0.065	0.045	0.487	0.282	1.100	0.640

Table 15. Biometric data for *Kaltenbachiella nirecola*, first instar larva borne by the emigrant.

Number	BL	BW	HFL	HTIL	HTAL	TAL	URSL	ASL	BW/BL	TAL/BL	TAL/HFL	URSL/HFL
1	0.461	0.195	0.109	0.091	0.046	0.119	0.058	0.041	0.423	0.258	1.093	0.535
2	0.472	0.193	0.122	0.096	0.051	0.117	0.066	—	0.409	0.247	0.958	0.542
3	0.466	0.208	0.112	0.092	0.051	0.122	0.061	0.041	0.446	0.261	1.091	0.545
4	—	—	0.113	0.094	0.051	0.114	0.061	—	—	—	1.009	0.538
5	—	0.203	0.112	0.094	0.051	0.109	0.061	0.041	—	—	0.977	0.545
6	—	—	0.117	0.096	0.051	0.118	0.061	0.041	—	—	1.013	0.522
7	—	—	0.116	0.095	0.046	0.114	0.061	—	—	—	0.987	0.526
8	—	—	0.119	0.096	0.053	0.127	0.066	0.039	—	—	1.064	0.553

Table 16. Biometric data for *Kaltenbachiella elsholtriae*, first instar larva borne by the emigrant(skins).

Number	HFL	HTIL	HTAL	TAL	URSL	ASL	TAL/HFL	URSL/HFL
1	0.096	0.079	0.041	0.091	0.076	0.046	0.95	0.79
2	0.096	0.076	—	0.091	0.076	0.046	0.95	0.79
3	0.096	0.079	0.044	0.096	0.076	0.046	1.00	0.79

Table 17. Biometric data for *Paracolopha morrisoni* exule adult.

Number	BL	BW	HFL	HTIL	HTAL	HC	TAL	A III	A IV	A V	URSL	W IIIl
1	1.69	1.03	0.286	0.199	0.071	0.046	0.173	0.041	0.025	0.048	0.150	0.066
2	1.70	1.13	0.286	0.196	0.066	0.039	0.148	0.030	0.025	0.043	0.123	0.056
3	1.48	1.04	0.235	0.156	0.056	0.037	0.133	0.030	0.022	0.035	0.111	0.051
4	1.71	—	0.286	0.193	0.061	0.039	0.143	0.035	0.026	0.041	0.119	0.051
5	1.80	1.16	0.306	0.219	0.082	0.048	0.189	0.033	0.030	0.046	0.143	0.071
6	—	—	0.316	0.230	0.082	0.050	0.158	0.035	0.025	0.049	0.143	0.077
7	—	—	0.316	0.240	0.082	0.054	0.190	0.041	0.033	0.046	0.143	0.066
8	—	—	0.306	0.214	0.077	0.046	0.204	0.051	0.030	0.046	0.145	—
9	1.57	1.01	0.316	0.219	0.082	0.051	0.224	0.056	0.035	0.055	0.153	—
10	—	—	0.326	0.214	0.082	0.050	0.186	0.041	0.033	0.041	0.143	—

HC-Length of hind claw. W IIIl-Maximal diameter of lateral wax gland plate on abdominal tergite III.

Table 18. Biometric data for *Paracolopha takahashii* exule adult.

Number	BL	BW	HFL	HTIL	HTAL	HC	TAL	A III	A IV	A V	URSL	W IIIs	W IIIl
1	1.50	0.79	0.194	0.163	0.056	0.021	0.191	0.041	0.030	0.053	0.125	0.034	0.051
2	1.25	0.66	0.224	0.201	0.061	0.025	0.204	0.049	0.032	0.066	0.138	0.051	0.071
3	—	—	0.221	0.184	0.062	0.021	0.168	0.035	0.034	0.061	0.122	—	—
4	1.30	0.67	0.223	0.194	0.062	0.024	0.189	0.041	0.035	0.063	0.133	0.051	0.082
5	—	—	0.245	0.237	0.071	0.025	0.224	0.051	0.041	0.076	0.133	0.051	0.092

W IIIs-Maximal diameter of spinal wax gland plate on abdominal tergite III.

Table 19. Biometric data for *Colopha kansugei*, exule adult.

Number	BL	BW	HFL	HTIL	HTAL	HC	TAL	A III	A IV	A V	URSL	W IIIs	W IIIl
1	1.33	0.82	0.132	0.101	0.034	0.016	0.112	0.020	0.018	0.025	0.051	0.030	0.025
2	1.32	0.77	0.132	0.094	0.030	0.018	0.113	0.023	0.015	0.026	0.052	0.020	0.020
3	1.35	0.82	0.122	0.086	0.030	0.016	0.117	0.025	0.017	0.028	0.051	0.017	0.020
4	1.25	0.81	0.122	0.086	0.030	0.015	0.106	0.020	0.015	0.023	0.046	0.026	0.020
5	1.31	0.71	0.112	0.084	0.026	0.015	0.099	0.020	0.015	0.025	0.051	0.025	0.024
6	1.48	0.77	0.162	0.125	0.033	0.018	0.127	0.025	0.020	0.033	0.061	0.039	0.035
7	1.36	0.66	0.130	0.094	0.030	0.015	0.098	0.020	0.012	0.025	0.053	0.031	0.030
8	1.56	0.76	0.177	0.130	0.041	0.021	0.132	0.031	0.021	0.030	0.059	0.034	0.040
9	1.56	0.82	0.177	0.127	0.041	0.021	0.141	0.028	0.025	0.030	0.058	0.030	0.035
10	1.49	0.79	0.200	0.152	0.048	0.019	0.142	0.033	0.023	0.030	0.058	0.043	0.044
11	1.54	0.85	0.176	0.135	0.046	0.020	0.143	0.035	0.020	0.030	0.059	0.037	0.038

Table 20. Biometric data for *Kaltenbachiella nirecola*, exule adult.

Number	BL	BW	HFL	HTIL	HTAL	HC	TAL	A III	A IV	A V	URSL	W IIIs	W IIIl
1	1.63	1.28	0.319	0.265	0.071	0.025	0.209	0.042	0.041	0.056	0.081	0.049	0.069
2	1.45	1.07	0.316	0.275	0.074	0.029	0.194	0.046	0.040	0.051	0.076	0.045	0.062
3	1.64	1.26	0.316	0.265	0.076	0.034	0.204	0.046	0.041	0.051	0.074	0.049	0.077

Table 21. Biometric data for *Kaltenbachiella elsholtriae*, exule adult.

Number	BL	BW	HFL	HTIL	HTAL	HC	TAL	A III	A IV	A V	URSL	W IIIs	W IIIl
1	1.29	0.89	0.235	0.175	0.053	0.025	0.161	0.032	0.034	0.041	0.096	0.030	0.035
2	1.37	1.02	0.224	0.168	0.051	0.024	0.135	0.048		0.041	0.087	0.029	0.033
3	1.13	0.90	0.222	0.173	0.041	0.024	0.145	0.051		0.041	0.091	0.029	0.030

Table 22. Biometric data for *Paracolopha morrisoni* fundatrix adult.

Number	BL	BW	HFL	HTAL	TAL	A III	A IV	URSL	BW/BL	TAL/BL	TAL/HFL
1	1.68	1.18	0.32	0.091	0.18	0.071	0.045	0.101	0.70	0.11	0.57
2	1.64	1.08	0.31	0.091	0.19	0.068	0.049	0.101	0.66	0.12	0.61
3	1.71	1.18	0.33	0.091	0.18	0.071	0.045	0.101	0.69	0.11	0.56
4	1.62	1.21	0.30	0.088	0.16	0.060	0.035	0.096	0.75	0.10	0.54
5	1.52	1.06	0.28	0.079	0.16	0.050	0.038	0.096	0.70	0.10	0.55
6	1.67	1.16	0.31	0.085	0.17	0.066	0.043	0.101	0.70	0.10	0.55
7	1.57	1.13	0.31	0.081	0.16	0.063	0.040	0.091	0.72	0.10	0.53

Table 23. Biometric data for *Kaltenbachiella japonica*, fundatrix adult.

Number	BL	BW	HFL	HTAL	TAL	A III	A IV	URSL	BW/BL	TAL/BL	TAL/HFL
1	1.64	1.25	0.27	0.066	0.139	0.040	0.035	0.076	0.77	0.08	0.51
2	1.95	1.55	0.29	0.066	0.174	0.055	0.045	0.076	0.79	0.09	0.59
3	1.67	1.29	0.28	0.071	0.161	0.046	0.044	0.073	0.78	0.10	0.58
4	1.91	1.63	0.31	0.076	0.186	0.050	0.058	0.076	0.85	0.10	0.60
5	1.89	1.58	0.32	0.076	0.202	0.066	0.045	0.075	0.83	0.11	0.63
6	1.94	—	0.32	0.086	0.192	0.060	0.047	0.076	—	0.10	0.59

Table 24. Biometric data for *Kaltenbachiella spinosa*, fundatrix adult.

Number	BL	BW	HFL	HTAL	TAL	A III	A IV	URSL	BW/BL	TAL/BL	TAL/HFL
1	2.04	1.55	0.30	0.067	0.186	0.066	0.040	0.081	0.76	0.09	0.63
2	1.60	1.25	0.28	0.070	0.193	0.057	0.045	0.078	0.78	0.12	0.68
3	1.68	1.49	0.28	0.071	0.181	0.045	0.052	0.073	0.89	0.11	0.64
4	1.98	1.63	0.32	0.081	0.207	0.076	0.049	0.078	0.82	0.10	0.64

Table 25. Biometric data for *Kaltenbachiella nirecola* fundatrix adult.

Number	BL	BW	HFL	HTAL	TAL	A III	A IV	URSL	BW/BL	TAL/BL	TAL/HFL
1	2.06	1.78	0.33	0.076	0.227	0.101	0.045	0.078	0.86	0.11	0.68
2	2.17	1.69	0.35	0.086	0.227	0.086	0.050	0.081	0.78	0.10	0.64
3	1.73	1.63	0.31	0.071	0.186	0.076	0.040	0.076	0.94	0.11	0.60

Table 26. Biometric data for *Kaltenbachiella glabra* fundatrix adult.

Number	BL	BW	HFL	HTAL	TAL	A III	A IV	URSL	BW/BL	TAL/BL	TAL/HFL
1	2.05	1.57	0.33	0.076	0.171	0.055	0.040	0.077	0.77	0.17	0.52
2	1.68	1.26	0.38	0.076	0.207	0.060	0.045	0.081	0.75	0.25	0.54
3	1.73	1.48	0.30	0.066	0.176	0.050	0.038	0.078	0.86	0.20	0.58
4	2.04	1.88	0.34	0.071	0.181	0.048	0.038	0.073	0.92	0.18	0.54

Table 27. Number of cells in a wax gland plate (except for central fields).

Species (stage examined)	Prothorax		Ab. ter. I			Ab. ter. III			Ab. ter. V			Ab. ter. VII	
	sp.	lat.	sp.	pl.	lat.	sp.	pl.	lat.	sp.	pl.	lat.	sp.	lat.
Paracolopha morrisoni (emigrant progeny)	10—12	9—15	6—9	7—14	12—15	9—12	10—14	12—19	7—10	—	13—17	10—14	8—10
P. takahashii (exule adult)	?	?	10—13	12—14	17—26	9—14	12—16	20—28	13—22	—	24—26	20—23	18—19
Colopha kansugei (exule 1st instar larva)	4—8	8—11	4—7	4—8	6—10	4—8	5—8	7—9	6—8	4—9	7—12	8—12	14—19
Kaltenbachiella nirecola													
(emigrant progeny)	5—8	13—17	5—7	5—8	12—14	5—8	5—7	12—14	6—10	5—6	11—12	6—9	5—6
(exule adult)	8—10	19—23	6—8	9—10	13—19	6—10	7—10	12—17	6—10	8—9	12—15	9	7
K. elsholtriae (exule adult)	5—7	10—12	4—5	5—6	6—8	5	4—5	6—7	4—5	4—5	6	0 or 3	—

PLATES

Plate I

Fig. 29. Wax gland plates of *Paracolopha morrisoni* exule adult. A and B: collected in North America; spinal one (A) and lateral one (B) on abdominal tergite III [courtesy of Dr. R.L. Blackman]. C and D: collected in Japan; spinal one (C) and lateral one (D) on abdominal tergite III.

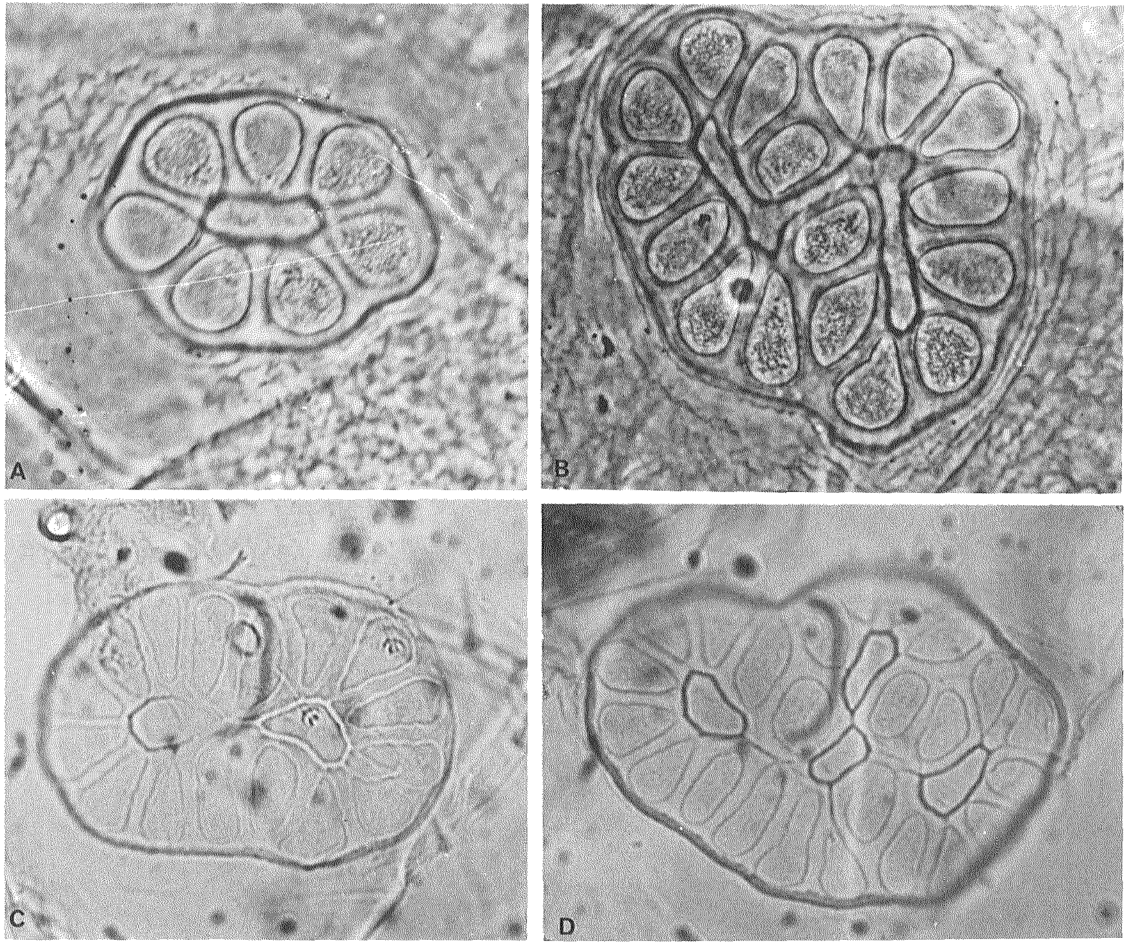

A
B
C
D

Plate II

Fig. 30. A : Fundatrix first instar larvae of *Paracolopha morrisoni* and hollows formed on the underside of a young leaf of *Zelkova serrata* [photographed on 25 May, 1984 in the campus of Hokkaidô Univ.], B and C : Galls of *Paracolopha morrisoni* [photographed on 7 June, 1984 in the campus of Hokkaidô Univ.]

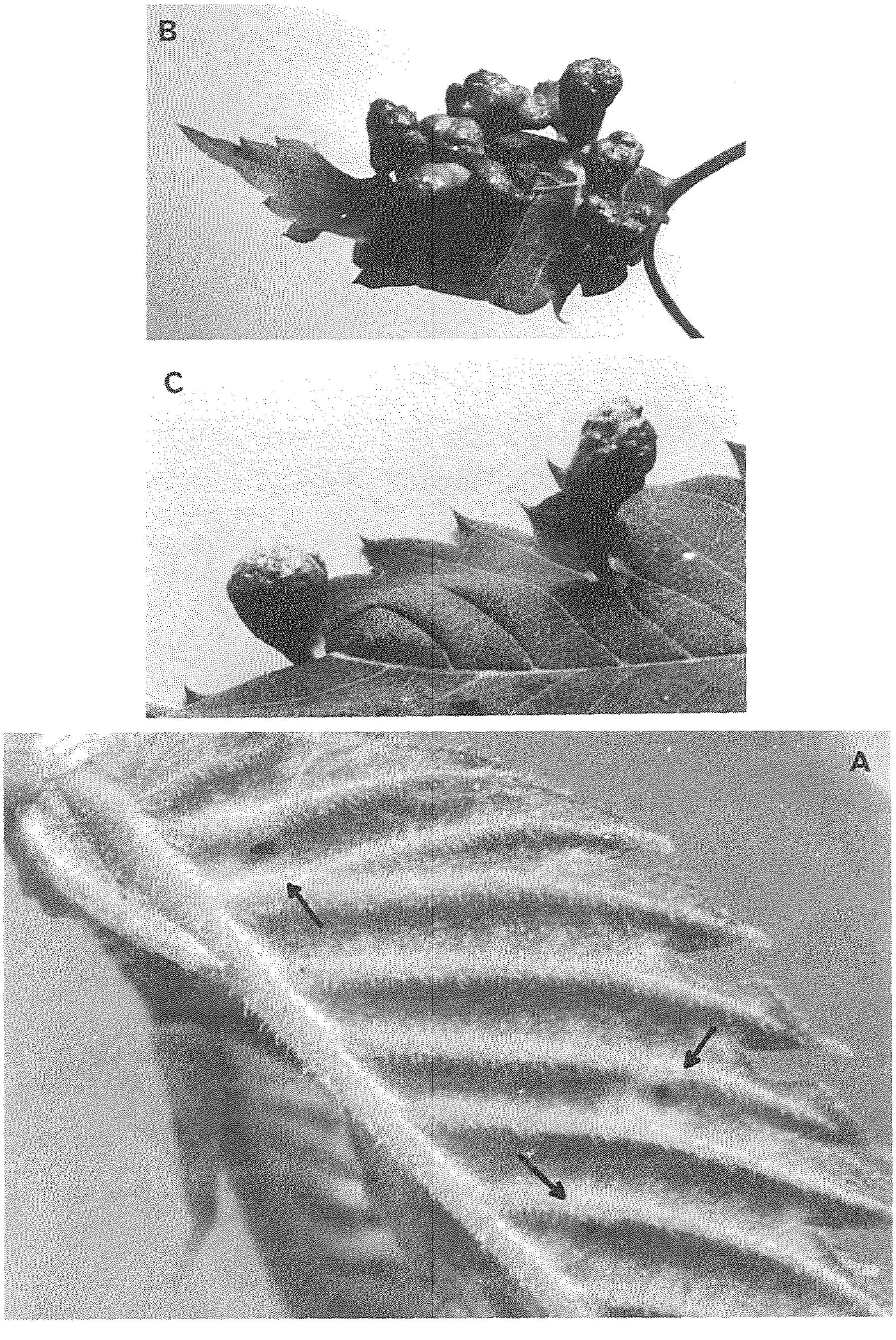

B
C
A

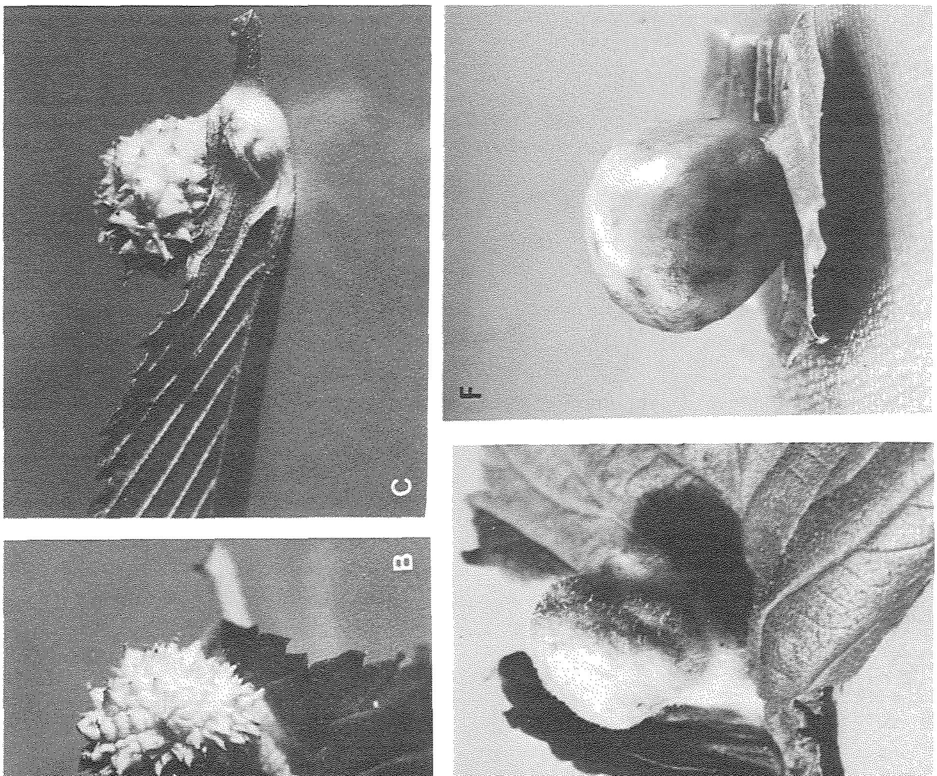
Plate III

Fig. 31. A and B: Early gall of *Kaltenbachiella japonica*. The fundatrix larva resides within the swollen part of the midrib in the underside (A). When viewed from dorsum the midrib has a slight projection only (B) [photographed on 7 June, 1984 in the campus of Hokkaidô Univ.], C and D: Galls of *Kaltenbachiella japonica*. On the twig with high gall density, galls are appressed together in cluster along the midrib (D) [photographed in the campus of Hokkaidô Univ. on 12 (D) and 14 (C) July, 1984].


A
B
C
D

Plate IV

Fig. 32. A : Gall of *Kaltenbachiella japonica* [photographed in the campus of Hokkaidô Univ. on 12 July, 1984], B and C : Gall of *Kaltenbachiella spinosa* [photographed on 12 July, 1984 ; collected in Bibai, Hokkaidô], D and E : Gall of *Kaltenbachiella nirecola* [photographed on 14 July, 1984 ; collected in Bibai, Hokkaidô], F : Gall of *Kaltenbachiella glabra* [specimens submerged in 70% alcohol ; courtesy of Dr. S. Aoki].


A
B
C
D
E
F