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QUEEN POLYMORPHISM IN A NON-PARASITIC *LEPTOTHORAX* SPECIES (HYMENOPTERA, FORMICIDAE)

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SUMMARY

Queen polymorphism, the occurrence of several morphologically distinct forms of reproductive females within one species, has been reported in several Ponerinae, and in some mostly socially parasitic Formicinae and Myrmicinae. We report here the first record of a queen polymorphism in a non-parasitic leptothoracine species. Dealate gynomorphic as well as intermorphic and nearly ergatomorphic specimens are found to be the reproductive queens in several populations of this species along St. Lawrence River, Quebec, Canada. The species is functionally monogynous, having only one reproductive female in each colony, and often one or several inseminated but not egg-laying potential queens. Intermorphs may have identical offspring, or produce both intermorphs and gynomorphs as young potential queens. A genetical origin of this queen polymorphism, as in *Harpagoxenus sublaevis*, is suggested. The species is related to *Leptothorax muscorum* (Nyl.), but not yet definitely identified. The queen polymorphism is described, the known range of the phenomenon and preliminary results of breeding experiments are recorded.

ZUSAMMENFASSUNG

Königinnenpolymorphismus bei einer nichtparasitischen Leptothorax-**Art (Hymenoptera, Formicidae)**

Königinnenpolymorphismus, das Vorkommen mehrerer morphologisch verschiedener Formen von reproduktiven Weibchen innerhalb einer Art, ist von einigen Ponerinen sowie zumeist sozialparasitischen Formicinen und Myrmicinen bekannt. Wir berichten hier über das erste Beispiel von Königinnenpolymorphismus bei einer selbständigen Leptothoracinen-Art. Entflügelte gynomorphe, intermorphe und nahezu ergatomorphe Tiere sind als reproduktive Königinnen in einigen Populationen dieser Art entlang dem St. Lorenzstrom in Quebec, Kanada, zu finden. Die Art ist funktionell monogyn, hat also nur jeweils ein reproduktives Weibchen in jedem Volk, dazu oft eine oder mehrere begattete, aber nicht legende potentielle Königinnen. Eine Königin einer bestimmten

Morphe kann gleichartige Nachkommen haben, eine andere Morphe, oder auch beide nebeneinander als potentielle Jungköniginnen produzieren. Wir vermuten eine genetische Grundlage für den Königinnenpolymorphismus dieser Art, wie bei *Harpagoxenus sublaevis* nachgewiesen. Die Art ist mit *Leptothorax muscorum* (Nyl.) verwandt, jedoch nicht endgültig determiniert. Der Königinnenpolymorphismus wird beschrieben, seine bisher bekannte Verbreitung und vorläufige Ergebnisse von Zuchtversuchen werden mitgeteilt.

INTRODUCTION

In most species of ants the queen is easily distinguished from the worker caste by its morphology. It has three ocelli, a thorax with clearly separate pro-, meso-, meta- and epinotum, and two pairs of wings which are shed after mating.

The worker on the other hand has no traces of wings, and its thorax is much smaller with the sclerites widely fused. The ocelli are absent in many species, particularly in the Myrmicinae.

Several ant species are known, however, where the queen is ergatoid, i.e. workerlike, or where a queen polymorphism does occur, in that two or more morphologically different female forms may function as reproductives. In such species it is sometimes difficult to tell apart queen and worker by morphology. BUSCHINGER & WINTER (1976) therefore have proposed to restrict the terms " queen " and " worker " to designate the role, and thus caste (MICHENER, 1974), of an individual, and to denote its morphological aspect as gynomorphic, intermorphic, or ergatomorphic, irrespective of its function.

Ergatomorphic or more or less intermorphic females as the only queen morphs are quite frequent in more primitive ant subfamilies, like the Cerapachyinae and Ponerinae (for a survey see HASKINS & WHELDEN, 1965). Such queens have been reported also from several myrmicine ants, especially from species of the *Monomorium salomonis* - group (BOLTON, 1986). A queen polymorphism, however, with several queen morphs within one species, is apparently rare. Occasionally intermorphs have been found in species with gynomorphic queens, like *Myrmica rubra* (BRIAN, 1955), *Leptothorax acervorum* (BERNARD, 1948, 1951), *L. gredleri* (BUSCHINGER, 1974 a), *L. nylanderi* (PLATEAUX, 1970), *Harpagoxenus americanus* (BUSCHINGER & ALLOWAY, 1977), and *H. canadensis* (BUSCHINGER & ALLOWAY, 1978). These either lack a spermatheca or have at least not been found inseminated and fertile (A.B., unpubl. results).

Queen polymorphism with gynomorphic, intermorphic, and/or ergatomorphic reproductive females has been described in *Rhytidoponera metallica* (HASKINS & WHELDEN, 1965 ; HÖLLDOBLER & HASKINS, 1977), and in *Hypoponera eduardi* (LE MASNE, 1953, 1956).

With the exception of the afrotropical *Monomorium rufulum,* in which both apterous and alate emales are produced (BOLTON, 1986), in the higher subfamilies, Myrmicinae and Formicinae, queen polymorphism appeared to be restricted to certain socially parasitic species. In the Formicinae, it was found in *Polyergus rufescens* (STITZ, 1939 and personal observations of A.B.), and in *Aporomyrmex ampeloni* (FABER, 1969). Among the Myrmicinae, the guest ants of the genus *Formicoxenus,* living in nests of *Formica* and *Myrmica* species, apparently all have polymorphic queens (FRANCŒUR *et al.,* 1985), and in the slavemaking ant, *Harpagoxenus sublaevis,* a genetical origin of queen polymorphism has been demonstrated (BUSCHINGER, 1978 ; WINTER & BUSCHINGER, 1986). The meaning of queen polymorphism is not yet understood. In Formicoxenus it might be adaptive in that the winged queens are able to reach and colonize distant host species nests, whereas the flightless ones are better fit for the continuous exploitation of the suitable habitat where they were born, with usually several closely neighboring host species nests. Queen polymorphism thus may be kept in balance by two counteracting selective forces. In *Harpagoxenus sublaevis,* queen polymorphism apparently represents a side-effect of a genetically mediated caste determination (WINTER & BUSCHINGER, 1986).

Quite unexpectedly, therefore, we recently found a polymorphic queen caste in a non-parasitic *Leptothorax* species from Quebec, Canada. The species in question is close to, but certainly not identical with, *Leptothorax muscorum* (Nyl.). The taxonomy of the North American species belonging to the subgenus *Leptothorax* s. str. (= *Mychothorax* Ruzsky) is quite in confusion. A revision of the group and the identification of our taxon will be provided by A. FRANCŒUR. We therefore refrain from giving a definite name yet, and will refer to it in the further text als *Leptothorax species A.*

MATERIAL AND METHODS

Complete colonies of *Leptothorax sp. A* and other related species were collected in early summer 1979 (BUSCHINGER), 1983 (BUSCHINGER, FRANCŒUR, ALLOWAY, STUART), and 1985 (BUSCHINGER, HEINZE) in Quebec in several localities along St. Lawrence and Saguenay Rivers *(fig. 1).* The ants nest in dry, decaying sticks on flat, sunexposed rocks which are partly covered by lichens and shrubs. Some were also found in light coniferous forests, and a few colonies were collected underneath small pebbles.

A total of 237 colonies were gathered. Some of them were directly stored in 70 % ethanol, others were kept alive in artificial nests (BUSCHINGER, 1974 b) over several breeding cycles.

To check the reproductive function of intermorphic females about 100 of them were dissected as described by BUSCHINGER & ALLOWAY (1978).

Measurements of length and width of thorax etc., and classification of thoracic structures, wing vestiges and ocelli were done with a Wild M5 dissecting microscope. About 200 queens and other females with spermatheca, inseminated or not, were examined, though not all measurements could be taken from each female. Thoracic

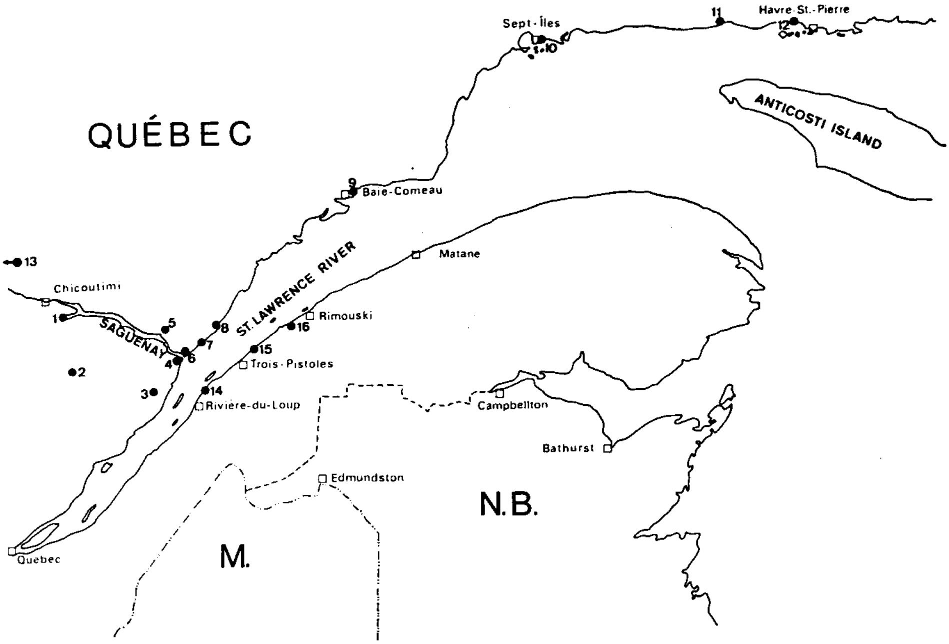

Fig. 1. — Map of southern Quebec. Collecting sites of *Lepthorax species A* and *B* are indicated. In all sites both species were collected.

Abb. 1. — Karte des südlichen Quebec. Die Fundorte für *Species A* und *B* sind angegeben. An allen angegebenen Punkten kamen beide Arten nebeneinander vor.

structures were classified following Buschinger & Winter (1975, for *Harpagoxenus sublaevis*), but adapted to the particular situation in *L. sp. A.* Skeletal elements of the thorax were named according to Wheeler (1910). The following discriminations were made (*fig. 2, 3*) :

0 : Ergatomorph, thorax of normal " worker ", promesonotal suture only slightly depressed, if at all.

1 : Intermorph, promesonotal suture strongly depressed.

2 : Intermorph, scutum separated from pro- and metanotum, the transscutal suture not clearly visible in the light microscope.

3 : Intermorph, scutum and scutellum separated by a deep suture. Traces of paraptera sometimes present.

4 : Gynomorph, thorax of ordinary alate female.

Due to the dark coloration of the head in *L. sp. A.*, ocellar structure could not be classified by its pigmentation. Only the relative size of the ocelli was recorded with the following ranks : no ocelli at all - minute depressions in the cuticle - small ocelli - large ocelli. The position of wing vestiges, if present, was also recorded.

Gynomorphic females of *L. sp. A* had to be told apart from the gynomorphs of another, sympatrical species, in which queen polymorphism apparently does not exist, by

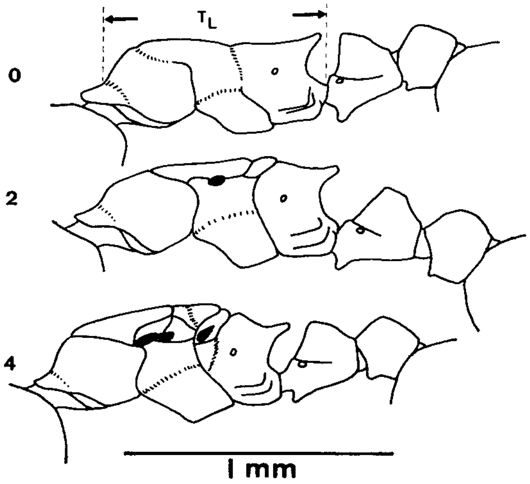

Fig. 2. — Alitrunk of ergatomorph, class 2 intermorph and gynomorph of *Leptothorax species A* in lateral view. TL = Length of thorax.

Abb. 2. — Thorax und Stielchen von Ergatomorphe, Intermorphe der Klasse 2 und Gynomorphe von *Leptothorax species A* in Seitenansicht. TL = Thoraxlänge.

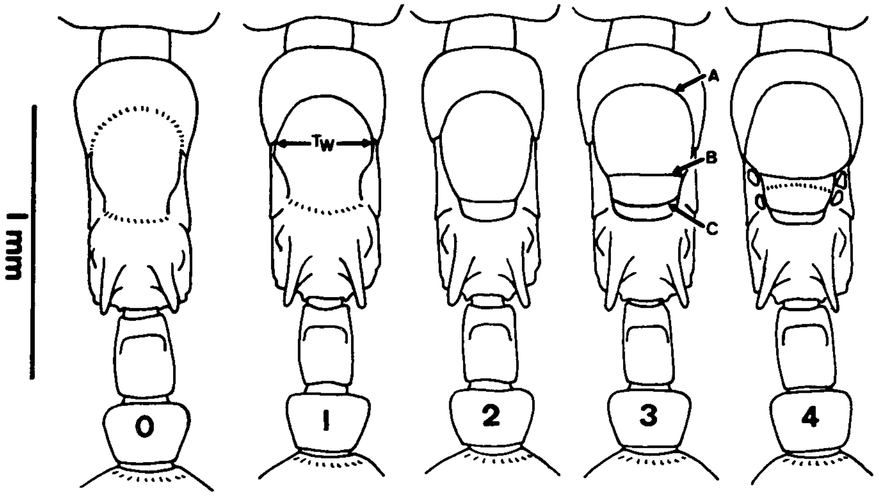

Fig. 3. — Alitrunk of *L. species A* ergatomorph (class 0), intermorphs (classes 1-3) and gynomorph (class 4), dorsal view. Tw = width of thorax. In the class 3 intermorph the arrows indicate the different sutures : A = promesonotal, B = transscutal, and C = mesometanotal sutures.

Abb. 3. — Thorax und Stielchen von Ergatomorphe (Klasse 0), Intermorphen (Klassen 1-3) und Gynomorphe (Klasse 4) von *L. species A* in Dorsalansicht. Tw = Thoraxbreite. Die Thoraxnähte sind in Klasse 3 durch Pfeile verdeutlicht : A : Promesonotalnaht, B : Transscutalnaht, C : Mesometanotalnaht.

morphological critera like coloration, shape and length of epinotal spines, and shape of petiole and postpetiole. In addition,, isozyme studies were done on ultrathin Polyacrylamide gels (0.2 mm), cast on polyester sheets (using the " flap " technique, RADOLA, 1980). pH-range was 4 to 8 and 3.5 to 9.5 (ampholines by Serva and LKB). Whole white pupae were crushed in 20 µl of a solution containing 20 % glycerol and 2 % Bromthymol Blue, and applied to the gel surface. Gels were run for approximately 5,000 Volthours, not exceeding 1,500 V. Gels were stained with Coomassie Brilliant Blue R 250, or using standard histochemical stains (SHAW & PRASAD, 1970 ; HARRIS & HOPKINSON, 1976, recipes slightly varied) for Isocitrate Dehydrogenase (IDH), Superoxide Dismutase (SOD), NAD dependent Malate Dehydrogenase (MDH), and others.

RESULTS

Evidence of queen polymorphism within *Leptothorax sp. A.*

Colonies of this species are usually small with often less than a dozen and rarely up to 100 adult individuals. Thus, it is quite easy to aspirate them completely, and to check their natural composition.

Among a total of 237 *Leptothorax* colonies collected in the field we found 144 colonies having an intermorphic queen. During the time of sampling the reproductives were easily recognized by their considerably extended gasters. 38 colonies with a gynomorphic dealate queen each, apparently belonged to the same species, *Leptothorax sp. A.* Their workers were of similar size and coloration, and no morphological differences could be found with the aid of a dissecting microscope. Finally, 55 colonies with gynomorphic queens apparently did belong to a second, larger species, with darker coloration in ♀♀ and ☿☿. It will be referred to as *Leptothorax sp. B.* in the further text.

Conspecifity of the colonies with intermorphic queens and the similar ones with gynomorphic queens is better demonstrated by eleven colonies among the 144 with intermorphic queens which either in addition contained several nonfertile gynomorphs, or intermorph and gynomorph pupae, which apparently were offspring of the intermorphic queens. No colonies, however, were found with gynomorphic queen and exclusively intermorphic offspring.

In laboratory culture several colonies were producing female offspring over up to seven subsequent breeding cycles (artificially shortened annual cycles, see BUSCHINGER, 1974 b). In all these experiments the offspring of a colony, and thus its queen, was identical in all breeding cycles :

— One colony, collected in June, 1983, at Baie-St.-Catherine, with intermorphic queen and intermorph and gynomorph pupae, was producing ergatomorphs, intermorphs and gynomorphs during four subsequent breeding cycles.

— A colony with intermorphic queen, collected June, 1983, at La Baie, produced ergatomorphs and exclusively intermorphic young queens in seven breeding cycles.

— A colony with gynomorphic queen (*species A*), collected June, 1983, in the Laurentides Park, over seven breeding cycles had always gynomorphic offspring together with ergatomorphs.

The same constancy in the composition of the offspring could be observed in all colonies collected in summer, 1985, and kept in captivity during two laboratory breeding cycles.

These observations clearly demonstrate that the production of gynomorphs and/or intermorphs is not due to laboratory conditions or environmental influences.

Like several other leptothoracine species (BUSCHINGER *et al.*, 1980), the intermorphic young females exhibit a sexual calling behavior when ready to mate. With the gaster somewhat erect and the stinger extruded they offer a sexual pheromone from the poison gland, which attracts and stimulates the alate males for copulation. Alate gynomorphs of *species A* exhibit an identical behavior, and male offspring of intermorphic queens is attracted both by calling intermorphs and gynomorphs. Mating occurs in laboratory. conditions. Thus, " crossbreeding " of sexual offspring of gynomorphs and intermorphs was possible.

In control experiments we observed that *species A*- ♂♂ were much less attracted by *species B* poison gland secretion than by the secretion of *species A* poison glands. European *L. muscorum* (Nyl.) females also have a sexual calling behavior (BUSCHINGER & ALLOWAY, 1978), but *species A*- ♂♂ again do not react to their pheromone.

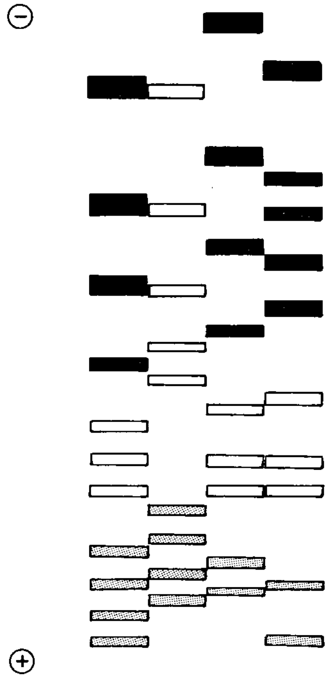

Fig. 4. — Schematic and simplified pattern of isoenzymes of nonspecific esterases in different *Leptothorax* species. Samples were applied near the cathode; pH-gradient is 4 to 8. Black bands indicate greater enzyme activity. Dotted bands correspond to allozymes on one locus in each species (see text). From left to right: *L. species A.*, *L. species B*, *L. acervorum*, *L. muscorum* from Europe.

Abb. 4. — Vereinfachtes Schema der Isoenzyme unspezifischer Esterasen verschiedener Lepthorax-Arten. Die Proben wurden nahe der Kathode aufgetragen; pH-Gradient 4 bis 8. Schwarze Banden zeigen stärkere Enzymaktivität an. Gerasterte Banden entsprechen verschiedenen Allozymen eines Locus innerhalb einer Art (vgl. Text). Von links nach rechts: *L. species A*, *L. species B*, *L. acervorum*, *L. muscorum* aus Europa.

Finally, preliminary results of electrophoretic studies also reveal that *species A* should represent a good species with polymorphic queen caste.

— Esterase IEF yields four to five major bands in *L. species A*, in *species B*, and in European *L. acervorum* and *muscorum* (*fig. 4*), which seem to be species-specific and quite invariable in all populations studied (37 colonies of *L. sp.* A from 10 different sites, 11 colonies of *sp. B* from 7 sites, and about 8 colonies each of *L. acervorum* and *L. muscorum* from sites near Nuremberg, Bavaria, and Nyehusen in Southern Sweden). No difference was found between *species A* colonies with intermorphic or gynomorphic queens (8 colonies with only gynomorphs, 5 with both gynomorph and intermorph offspring, and 24 with only intermorphs).

In addition to these invariable bands in all four species a set of variable bands was found ; one always appears in single (haploid) male pupae, one or two in female pupae, and one to three in whole colonies. These bands apparently represent allozymes of one locus. The bands (four in *L. sp. A*, four in *L. sp. B*, two in *L. acervorum* and *L. muscorum*) in each species have a different pI. No interspecific heterozygotes have been found.

— Isocitrate dehydrogenase (IDH) patterns are very similar in the major bands in *L. sp. A*, *L. acervorum* and *L. muscorum*. Only for *L. sp. B* a different pattern was found (*fig. 5*).

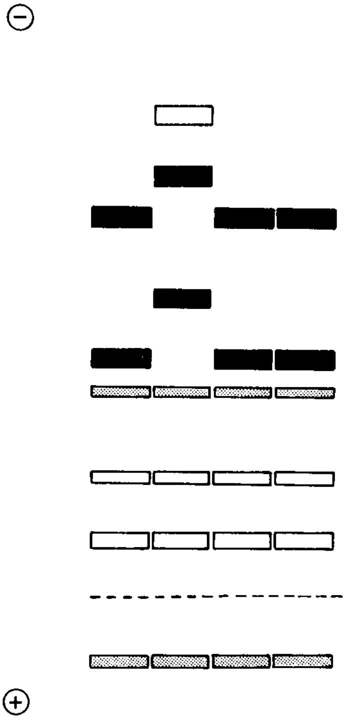

Fig. 5. — Schematic pattern of IDH (black and white bands) and SOD (dotted bands) isoenzymes. Application point is indicated by the dotted line. From left to right : *L. species A*, *L. species B*, *L. acervorum*, *L. muscorum*.

Abb. 5. — Schema der Isoenzymmuster von IDH (schwarze und weiβe Benden) und von SOD (gerasterte Banden). Die unterbrochene Linie gibt den Auftragungspunkt an. Von links nach rechts : *L. species A*, *L. species B*, *L. acervorum*, *L. muscorum*.

— In Superoxide dismutase (SOD) (= Tetrazolium oxidase) and other enzymes (not illustrated) clear species differences were not yet observed. Further investigations will be done.

These results strongly support a separate specific rank of *species A,* and also prove conspecifity of gynomorphic and intermorphic specimens of this taxon.

Analysis of queen polymorphism in *Leptothorax sp. A.*

Figures 2 and 3 illustrate the thoracic structures of ergatomorphs, intermorphs and gynomorphs of *L. sp. A.* The ergatomorph corresponds to the usual " worker " of other *Leptothorax* (s. str.) species. The intermorphs exhibit thoracic structures gradually changing from class 1 to 3 into the fully developed pterothorax of the gynomorph (class 4).

Some measurements were done to demonstrate the morphologically intermediate appearance of the intermorphic queens. *Species B* gynomorphs were included to show their size differences in comparison with *species A* (*table I*).

Intermorphic queens in general have a thorax length (TL) between that of ergatomorphs and gynomorphs, with mean values (0.93 mm) closer to those of ergatomorphs (0.88 mm) than to gynomorphs (1.01 mm). Their

Table I. — Thorax length and width of ergatomorphs, intermorphs and gynomorphs of *Leptothorax species A,* and gynomorphs of *L. species B,* in mm. Differences of TL/TW indices in class 1-4 specimens are statistically significant (U-test).

Tabelle I. — Thoraxlänge und - breite von Ergatomorphen, Intermorphen und Gynomorphen von *Leptothorax species A,* sowie Gynomorphen von *L. species B,* in mm. Die Unterschiede der TL/TW-Indices von Exemplaren der Klassen 1-4 sind statistisch signifikant (U-Test).

	Thorax length min-mean-max	Thorax width min-mean-max	Thorax length / Thorax width		n specimens checked
L. species A					
Ergatomorphs (0)	0.83 - 0.89 - 0.96	0.27 - 0.30 - 0.36	ca. 3.00		30
				n.s.	
Int. class 1	0.93	0.31	2.98		35
				< 0.01	
Int. class 2	0.84 - 0.93 - 1.05	0.27 - 0.33 - 0.39	2.87		57
				< 0.01	
Int. class 3	0.93	0.35	2.58		15
				< 0.01	
Gynomorphs (4)	0.87 - 1.01 - 1.19	0.38 - 0.46 - 0.53	2.19		42
L. species B				n.s.	
Gynomorphs (4)	0.94 - 1.12 - 1.24	0.45 - 0.53 - 0.62	2.09		61

Table II. — Correlation between the development of thorax and ocelli in intermorphic females of *Leptothorax species A.*

Tabelle II. — Korrelation zwischen der Ausprägung von Thorax und Ocellen bei intermorphen Weibchen von *Leptothorax species A.*

	Thorax class		
n and size of ocelli	1	2	3
2 minute	4 %	—	—
3 minute	12.5 %	10.5 %	—
2 minute, 1 medium	37.5 %	13.0 %	6.0 %
3 medium	46.0 %	76.5 %	94.0 %
n intermorphs checked	48	85	17

thorax width (TW) is even more like that of ergatomorphs (erg. 0.30, int. 0.31-0.35, gyn. 0.46 mm). Thus, the lower intermorphs of class 2 and 1 have quite a narrow thorax with an index TL/TW of 2.87 and 2.98 respectively, close to that of ergatomorphs (3.00). Intermorphs of class 3 are intermediate with a TL/TW index of 2.58 as compared to gynomorphs with 2.19.

In *table II* we tried to evaluate whether a correlation exists between the development of thorax and ocelli in intermorphic queens. Ergatomorphs in this species group usually have no traces of ocelli on their heads, whereas in gynomorphs three well developed, fullsized ocelli are present. Clearly the number and size of ocelli are growing in correlation with the thoracic class of the specimens. Wing vestiges of different size also may be present in intermorphic queens, and, like the ocelli, they are preferably found in higher class intermorphs (*table III*).

Table III. — Size and localization of wing vestiges in intermorphic females of *Leptothorax species A.*

Tabelle III. — Größe und Lage von Flügelrudimenten bei intermorphen Weibchen von *Leptothorax species A.*

	Thorax class		
Wing vestiges	1	2	3
none	58.0 %	36.0 %	5.5 %
front	19.0 %	45.0 %	50.0 %
hind	17.0 %	6.0 %	—
2 pairs	6.0 %	9.0 %	11.0 %
Wing stumps			
front	—	3.0 %	28.0 %
hind	—	—	—
2 pairs	—	1.0 %	5.5 %
n intermorphs checked	52	98	18

In their external morphology and size the intermorphic queens, thus, represent true intermediates between the ergatomorph and the gynomorph. Dissections of representative numbers of specimens were carried out in order to check the reproductive organs and to compare them with those of gynomorphs.

The results clearly demonstrated that all intermorphs had fully developed ovaries with 2 × 3 ovarioles and a spermatheca, without any visible difference to those of gynomorphs. The reproductive organs, thus, have the size and shape which is tpical for reproductive females of the genus. Ergatomorphs, on the contrary, never had a spermatheca, and their ovaries usually consisted of 2, rarely up to 5 ovarioles, as is also frequent in other *Leptothorax* pecies.

Evidence of functional monogyny in *Leptothorax sp. A.*

In about 25 % of the colonies collected we found more than one, and up to five females, either intermorphic or gynomorphic ones or both together. Dissectioning of all females of such colonies revealed that in all cases only one of them was egg-laying, whereas the others also had their receptacles filled with sperm, but their ovarioles were short and transparent like in virgin females. No yolk deposition could be seen in their oocytes.

One remarkable sample apparently consisted of two colonies which had been nesting in close vicinity, and thus were unfortunately aspirated together, which resulted in fighting among the ants. However, the sample contained two fully fertile intermorphs (the queens of the two colonies), nine inseminated but sterile intermorphs, and one gynomorph in the same reproductive state. So, in one of the original colonies, a potentially fertile gynomorph had been living alongside an intermorphic queen.

The " potential queens " certainly were living in the colonies, presumably their mother colonies, at least since the previous summer, since during the time of collecting the new sexual brood had not yet reached the adult instar. Such a presence of inseminated potential queens alongside of only one truly fertile queen was termed functional monogyny (Pardi, 1940, 1946 ; Buschinger, 1968). It is a frequent phenomenon in the guest ant genus *Formicoxenus* (Francœur *et al.*, 1985), but also occurs in *Leptothorax gredleri* Mayr (Buschinger, 1968), a close relative of *L. muscorum.*

Range of *Leptothorax species A* and frequency of intermorphic queens in different populations

In the map (*fig. 1*) the localities are indicated where we have collected colonies of *L. sp. A.* (*L. sp. B* was found in all these sites, too). Supposedly its actual range is much larger than is presently known, however, in some areas where we have collected, the species is apparently lacking. Thus, in quite dense and dark mixed and coniferous forests in the Gaspe peninsula (not indicated in the map), we only found *Lepthorax sp. B.* In acorn and hickory forests near Montreal (Mont Rigaud) with habitats apparently suitable for

L. sp. A, only *Myrafant* species were collected, and no species of the subgenus *Lepthorax* at all. Numerous *Leptothorax* colonies were sampled by one of us (A.B.) near Rouyn-Noranda in northern Quebec, around Mississauga, Ontario, and farther to the West including the Canadian and American Rocky Mountains. With the exception of one intermorphic female in a nest quite surely belonging to *L. sp. A* from Sioux Narrows (Ontario ; the site is not indicated on the map), no other intermorphic females were found in these places, but whether or not one of the forms observed there is identical with *L. sp. A* cannot yet be determined.

On the other hand, in some localities along St. Lawrence River, *L. sp. A* is by far the most common *Leptothorax* species. Thus, we found 126 colonies of *L. sp. A*, 20 of *L. sp. B*, and 8 colonies of *Harpagoxenus canadensis*, in the comparatively open, rocky areas around Tadoussac.

The frequencies of *L. sp. A* colonies with gynomorphic and intermorphic queens apparently vary in different localities (*table IV*). Populations with a particularly high percentage of colonies with intermorphic queens were mainly found along the shores of St. Lawrence and Saguenay Rivers, whereas the gynomorphic queens apparently dominate in some distance from the shores, e.g. in the Laurentides Park.

DISCUSSION

The *Leptothorax* species treated in this paper and provisionally named *L. sp. A* clearly represents a good species, living in sympatry with at least one related species (*L. sp. B*) from which it is told apart by morphological and biochemical means. A comparatively high numer of subspecies and varieties of *Lepthorax canadensis* Provancher have been described from North America (Creighton, 1950). All these forms later on were synonymized under *L. muscorum* (Nyl.) by Brown (1955), which surely does not match the actual situation. A systematical revision of all the group is urgently needed. Due to apparently widely overlapping morphological characters, a biosystematical approach using behavioral studies (sexual behavior and pheromones), karyological and biochemical cues will be most promising.

Within our *L. sp. A* we could demonstrate a queen polymorphism in that the reproductive function may be taken over by intermorphic specimens morphologically standing in between the usual dealate female and the worker (ergatomorph), as well as by normal dealate females.

So-called intercastes have been frequently reported to occur in many *Leptothorax* (subgenus *Leptothorax* sensu Smith, 1950 = *Mychothorax* Ruzsky) species, however, *L. sp. A* is the first exemple where a fully reproductive function, i.e. presence of a spermatheca full of sperm and egg-laying, of such intermorphs has been demonstrated in an independent leptothoracine.

Within this tribe, queen polymorphism occurs regularly in most (perhaps all ?) species of the guest ant genus *Formicoxenus* (FRANCŒUR *et al.*, 1985), including the former *Leptothorax diversipilosus* and *L. provancheri* (BUSCHINGER, 1979 ; BUSCHINGER *et al.*, 1980), and in the European slavemaker ant, *Harpagoxenus sublaevis* (BUSCHINGER, 1978 ; WINTER & BUSCHINGER, 1986). The frequency of gynomorphic queens in the latter is very low, with about 1 % of field colonies having a dealate queen, whereas all others have ergatomorphic or slightly intermorphic ones. In *Formicoxenus* the frequency of gynomorphic queens varies, dependent upon the species, but is usually higher than in *Harpagoxenus*. In *F. nitidulus*, e.g., about 20 % of the colonies have a gynomorphic queen.

In *Leptothorax sp. A*, gynomorphic queens apparently are even more frequent (*table IV*), but highly dependent upon the collecting sites. Thus, in a large population near Tadoussac only 14 of 94 colonies studied (= 15 %), did contain a dealate female, and only 10 of them were the colony queens, the remaining 4 colonies having intermorphic queens and a dealate gynomorph each in addition. In the Laurentides Park, on the contrary, there were

Table IV. — Frequency (%) of *Leptothorax species A* colonies with gynomorphic females in different collecting sites.

Tabelle IV. — Häufigkeit (%) von Völkern von *Leptothorax species A* mit gynomorphen Weibchen an verschiedenen Fundorten.

No in map (*fig. 1*)	Situated near to	N colonies checked	Colonies with gynomorphic females	
			n	%
1	Bagotville / La Baie	35	14	40
2	Laurentides Nat. Park	11	9	82
3	St. Siméon	7	3	43
4	Baie Ste. Catherine	3	1	—
5	Sacré Cœur du Saguenay	3	1	—
6	Tadoussac	94	14	15
7	Grandes Bergeronnes	6	2	33
8	Les Escoumins	3	1	—
9	Baie Comeau	4	0	—
10	Sept-îles	3	0	—
11	Magpie	1	0	—
12	Rivière Romaine	9	3	33
13	Ste. Monique du Lac St. Jean	2	1	—
14	Cacouna	2	0	—
15	Cap-à-l'-Original	4	1	25
16	Bic	1	1	—

gynomorphic queens in 9 of 11 colonies (80 %). Most probably the queen polymorphism of this species is genetically mediated as in *Harpagoxenus sublaevis,* which will be tested by breeding experiments.

A second interesting feature of *L. sp. A* is its functional monogyny. The presence of several inseminated but not egg-laying females alongside always only one fully fertile specimen in a colony, is common again in most, if not all, *Formicoxenus* species (FRANCŒUR *et al.,* 1985), but it is definitely lacking in the strictly monogynous *Harpagoxenus sublaevis* (BUSCHINGER, 1966; BUSCHINGER & WINTER, 1978). Up till present a functional monogyny, among the *Leptothoracini,* has only been found in one other independent species, *L. gredleri* Mayr (BUSCHINGER, 1968), which, however, has gynomorphic queens only.

The adaptive value of both functional monogyny and queen polymorphism is unknown yet. We may speculate that young females, after mating near the mother nest, may return to it, and perhaps take over the queen role when the old queen eventually dies. The chance to become a reproductive by this way may be similar to that of successfully founding an own colony.

Queen polymorphism in *Formicoxenus* was discussed as possibly adaptive in correspondence to life in the patchily distributed colonies of the host species (see introduction). In *Leptothorax sp. A,* which is independent, we suggest a similar explanation. Along the shores of St. Lawrence and Saguenay Rivers, where intermorphic queens are particularly frequent, this species lives in rocky areas with a light to sparse vegetation of coniferous trees and shrubs. Insolation there is much more intense than in the surrounding dense forest areas, which are not inhabited by *L. sp. A.* The rounded, rocky outcrops, however, usually have a very restricted area of several 100 to several 1000 m^2, with often some kilometres between such places. Therefore, it might be more advantageous for a young, inseminated female, to remain in the area where she was born, than risking to drift, during her swarming flight, into an uninhabitable area. A gene for flightless females there should have a selective advantage. This gene may be carried to new sites with sperm stored in the receptacles of alate females. Its frequency may vary with the different sizes of habitats, and in fact we found much less intermorphic queens in quite extended, sandy coniferous forests, e.g., in the Laurentides Park (*table IV*).

Presently, however, these interpretations must remain speculative. With field and laboratory studies being continued we hope to find out convincing explanations.

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