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Specific Differences in the Bionomic Characters of Bumblebees. A Comparative Review¹⁾

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(With 4 text-figures)

Contents

Introduction	391
1. Habitat preferences	393
2. Nest site preferences	394
3. Nest entrance camouflage	396
4. Aggressiveness	396
5. Preparation of the first brood cell	397
6. Additional provisions for the first cell	399
7. Honey pot prepared by the queen	401
8. Location and clutch size of cells built upon the first cell	401
9. Location of later cells	402
10. Position of, and number of eggs in the later cells	403
11. Pollen priming in the later cells	403
12. Pocket makers versus non-pocket makers	404
13. Arrangement of cocoons forming batches	408
14. Arrangement of batches	409
15. Honey storage	410
16. Pollen storage	411
17. Wax nest envelope	412
18. Wax production	413
19. Intranidal behavior	413
20. Flower visiting habits	414
21. Size difference among females	418
22. Production of sexual broods	419
23. Laying workers	420
24. Behavior of new born sexuals	421
25. Hibernation	423
26. Phenology and colony size	424
27. Colony cycle and social organization	426
28. Usurpation	431
Discussions	434
Summary	441
Acknowledgements	441
Literature cited	441

1) Dedicated to Dr. Kunio Iwata, "J.H. Fabre in Japan", at his 70th birthday.

Introduction

The present paper was first written as a brief introductory note for the descriptions of nests of some Japanese bumblebee species. In preparing the draft, it was felt that further studies of these interesting bees must be undertaken upon a sound comparative basis. This idea gave an impetus to prepare the paper as a separate review.

Many specific differences have been reported on diverse aspects of bumblebee habits. These may be the outcomes of either common phyletic descents or parallelisms mainly caused by adaptations to similar environmental conditions. But differentiation of these two possibilities must be preceded by accurate documentation of specific differences. Some of such differences certainly deal with real specific or supraspecific differences, but some others reflect either observational errors or behavioral plasticity which allows different expressions according to situations. For a better understanding of comparative bumblebee bionomics, we must gradually separate group specificities from observational ambiguities. Recently Michener (1974) made an attempt to put some previous controversies in order, but there are still many aspects to be resolved through careful observations and comparisons.

In connection with observational errors, there are two sources of ambiguities. One is that a particular habit is described by some authors but ignored by others, being either simply overlooked or not evoked under certain conditions. Another is failure to specify the species observed. Probably for the general bionomic resemblance among species, many authors describe several observed species jointly, without specifying which were sources of particular bionomic features, despite of some differences are often suggested by the context of descriptions. Some possible sources of discrepancies due to behavioral plasticity are as follows: Some behavioral features may be released or not, or may be modified, according to the following conditions. 1) Differences among local populations, either by inherent characteristics or by different responses to environmental conditions. 2) Differences between natural colonies and those reared under artificial conditions. 3) Differences due to colony ontogeny, divided for the temperate species into several phases, e.g. posthibernation, solitary (=subsocial in terminology by Michener 1974), polyergic (from appearance of first workers to that of sexual broods), reproductive (to disappearance of sexuals), decline (to extinction of all nest inhabitants except prehibernating queens), hibernation. 4) Intimately linked with the preceding item, differences due to colony structure, affected by colony size, worker brood ratio, presence or absence of the queen, her senescence, presence or absence of laying workers, amount of food stored, presence of parasites, commensals, etc.

Future reports should consider these sources of different results and should specify the conditions of observation, as far as possible. The present review is by no means a complete bibliographical survey. It was prepared based upon basic

works and recent papers available to me. It is possible that some of the controversies enumerated below have already been resolved in the papers inaccessible to me. It must also be stressed that the review was written mainly for comparative purposes. Numerous important papers were ignored or only briefly referred to, if they lacked comparative information, whereas some rather fragmentary observations were cited if they involved interesting comparative data. It was attempted to cover most, if not all, bionomic characters on which some specific differences have been reported. But no effort was undertaken to cite all species so far observed as to each character.

In the following pages observations are cited as authentic unless controversial records or reasonable objections exist. The papers not directly accessible are mentioned in the text with those from which they were cited.

Synopsis of the species cited: The names of species are given according to recent usages (for the European species mainly by Løken 1973, and for the Nearctic species by Burks 1951, partly Krombein 1967), with the names used by the original authors of bionomic records in parentheses. The species are arranged according to the subgeneric system by Richards (1968¹), *Thoracobombus* interpreted in a wider sense) and classified into three sections. Of these, perhaps only *Odontobombus* is a natural group, but these sections are convenient to group various subgenera for a practical purpose. Areas where the species were observed are indicated by abbreviations (E=Europe, J=Japan, NA and SA=North and South America). Each subgenus is preceded by the abbreviation, which is used throughout the subsequent pages.

Section *Odontobombus* Krüger

- Dv Diversobombus* Skorikov: *diversus* Smith (J).
Fv Fervidobombus Skorikov: *atratus* Franklin (SA), *bellicosus* Smith (SA), *brasiliensis* Lepeletier (SA), *californicus* Smith (NA), *fervidus* (Fabricius) (NA), *medius* Cresson (NA), *mexicanus* Cresson (Costa Rica), *morio* (Swedrius) (SA), *pennsylvanicus* (De Geer) (NA,=*americanorum*), *pullatus* Franklin (Costa Rica), *transversalis* (Olivier) (SA,=*incarnum*).
Mg Megabombus Dalla Torre (= *Hortobombus* Vogt): *argillaceus* Scopoli (E), *consobrinus* Dahlbom (E), *gerstaeckeri* Morawitz (E), *hortorum* (Linné) (E), *runderatus* (Fabricius) (E).
Rh Rhodobombus Dalla Torre (= *Pomobombus* Vogt): *elegans* Seidl (E,=*mesomelas*), *pororum* (Panzer) (E).
Sb Subterraneobombus Vogt: *appositus* Cresson (NA), *borealis* Kirby (NA), *distinguendus* Morawitz (E), *subterraneus* (Linné) (E,=*laterillelus*).
Th Thoracobombus Dalla Torre (= *Agrobombus* Vogt): *humilis* (E,=*helferanus*, *variabilis*), *inexpectatus* (Tkalcú) (E), *muscorum* (Linné) (E), *pascuorum* (Scopoli) (E,=*agrorum*), *pseudobaicalensis* Vogt (J), *runderarius* (Müller) (E,=*derhamellus*), *schrencki* Morawitz (J), *sylvarum* (Linné) (E), *veteranus* (Fabricius) (E,=*equestris*).

Section *Anodontobombus* Krüger

- Al Alpinobombus* Skorikov: *alpinus* (Linné) (E), *arcticus* Kirby (E, var. *alpiniformis*), *balteatus* Dahlbom (NA, E,=*kirbyellus*), *polaris* Curtis (NA, according to Løken 1973, a

1) Milliron (1961, '71) and Tkalcú (1972) proposed other systems.

synonym of *arcticus* var. *alpiniformis*. Here conveniently regarded as an independent species).

Bo Bombus Latreille: *affinis* Cresson (NA), *hypocrita* Pérez (J), *ignitus* Smith (J), *lucorum* (Linné) (E), *magnus* Vogt (E), *occidentalis* Greene (NA), *terrestris* (Linné) (E), *terricola* Kirby (NA).

Kl Kalobombus Dalla Torre (= *Soroceansibombus* Vogt): *soroceansis* (Fabricius) (E).

Ml Melanobombus Dalla Torre (= *Lapidariobombus* Vogt): *alticola* Kirby (E), *lapidarius* (Linné) (E).

Pr Pyrobombus Dalla Torre (= *Pratobombus* Vogt): *ardens* Smith (J), *bifarius* Cresson (NA, ssp. *nearcticus* Handlirsch), *bimaculatus* Cresson (NA), *flavifrons* Cresson (NA), *frigidus* Smith (NA), *huntii* Greene (NA), *hypnorum* (Linné) (E), *impatiens* Cresson (NA), *jonellus* (Kirby) (E), *lapponicus* (Fabricius) (E), *mixtus* Cresson (NA), *pratorum* (Linné), (E), *perplexus* Cresson (NA), *sylvicola* Kirby (NA), *ternarius* Say (NA), *vagans* Smith (NA).

Rf Rufipedibombus Skorikov: *rufipes* Lapeletier (Java).

Section *Boopobombus* Frison

Ag Alpigenobombus Skorikov: *wurfleini* Radoszkowski (E, = *mastrucatus*).

Bb Bombias Robertson: *auricomus* (Robertson) (NA, conveniently treated as an independent species, not as a subspecies of *nevadensis*), *nevadensis* Cockerell (NA).

Cf Confusibombus Ball: *confusus* Schenck (E).

Cl Cullumanobombus Vogt: *cullumanus* (Kirby) (E), *rufocinctus* Cresson (NA).

Md Mendacibombus Skorikov: *mendax* Gerstäcker (E).

Rb Robustobombus Skorikov: *robustus* Smith (SA).

Sp Separatobombus Frison: *crotchii* Cresson (NA), *griseocollis* (De Geer) (NA, = *separatus*), *morrisoni* Cresson (NA).

1. Habitat preferences

The preferences for particular habitats, e.g. forests or openlands, have been recorded for many species. When the range of a species coincides with an extensive continental area of mild relief and monotonous vegetation, the habitat preference can be expressed geographically (e.g. Skorikov 1931, Moure and Sakagami 1962). In the areas with diverse habitats, however, different preferences may exist among the species inhabiting the same area (e.g. Hobbs 1964b~1968, Province of Alberta; Løken 1973, Scandinavia). Dealing with Balkan species, Pittioni (1938) distinguished four habitat preferences: eremophilous (grassland and bushes), orophilous (arid slopes above as well as below timber line), hylophilous (forests of both lowlands and high altitudes), and crystallophilous (humid valleys and high altitudes between timber and snow lines). This system was applied by Postner (1952) to various species living in a limited area (Erlangen and the vicinity). Recently K.W. Richards (1975) developed a more precise method to measure the habitat preferences of the species inhabiting a limited area of Alberta. The restricted distribution of some taxa is also known. *Alpinobombus* is famous by its borealpine distribution (Pittioni 1937, 1942b-'43, O.W. Richards 1931, K.W. Richards 1973, Skorikov 1937). *Cl. cullumanus* is rare and confined to chalk lands in

England (Alford 1975). *Fv. transversalis* is the unique species adapted to the tropical rain forest (Dias 1958, Moure and Sakagami 1962).

2. Nest site preferences

The preference for above ground nest sites has been recorded in some species. In Europe *Pr. hypnorum* is characterized by its frequent utilization of tree hollows, bird boxes, etc. (Postner 1952, etc.) Dias (1960, *Fv. atratus*) and Janzen (1971, *Fv. pullatus*) gave some discussions. According to K.W. Richards (1975), this tendency is commoner than so far assumed (cf. below). But above ground nesting is rarer and less differentiated than in the other three groups of Apidae (Euglossini, Meliponini and Apini). Many previous records concern with nests found on soil surface or in underground cavities. In the latter case, preexisting cavities and canals are always used. Later elaboration of cavity and canal walls is practiced. But except the preparation of hibernacula (cf. 25), nest burrows are not self-excavated. This lack of ability to excavate the own nest burrows is almost the only trait common to four tribes of Apidae (Zucchi et al. 1969), separating them from the related Anthophoridae.

Specific differences in nest site preferences have been recorded by many authors, though rarely quantitatively. Only some instances are cited:

A. Principally surface nesters (asterisk=the tendency less fixed): *Bo. lucorum*, *terrestris*, *Mg. hortorum*, *runderatus*, *Ml. lapidarius*, *Sb. subterraneus* (Sladen 1912); *Bo. affinis*, *terricola*, *Pr. impatiens* (Plath 1934); *Bo. lucorum*, *terrestris*, *Mg. hortorum*, *Ml. lapidarius* (Free and Butler 1959); *Al. polaris* (Richards 1973), *Bo. affinis*, *Pr. bimaculatus**, *impatiens**, *perplexus* (Milliron 1971); *Ag. wurfleini*, *Bo. lucorum*, *magnus*, *terrestris*, *Kl. soroeensis*, *Mg. hortorum*, *Sb. distinguendus*, *subterraneus* (Løken 1973); *Bo. lucorum*, *terrestris*, *Kl. soroeensis*, *Mg. hortorum**, *runderatus*, *Sb. distinguendus**, *subterraneus* (Alford 1975).

B. Principally surface nesters: *Cf. confusus*, *Pr. hypnorum**, *jonellus*, *Th. muscorum*, *pascuorum*, *runderarius*, *sylvarum** (Sladen 1912); *Fv. pennsylvanicus*, *Pr. bimaculatus* (Plath 1934); *Th. muscorum*, *pascuorum*, *runderarius* (Free and Butler 1959), *Fv. fervidus**, *pennsylvanicus** (Milliron 1971); *Pr. hypnorum**, *Th. muscorum*, *pascuorum*, *runderarius*, *sylvarum*, *veteranus* (Løken 1973); *Th. humilis*, *pascuorum*, *runderarius*, *sylvarum** (Alford 1975); *Fv. atratus*, *morio* (Zucchi unpub.).

C. Species recorded as quite plastic on nest preferences: *Pr. pratorum* (Sladen 1912); *Fv. fervidus*, *Pr. vagans* (Plath 1934); *Pr. pratorum*, *Th. sylvarum* (Free and Butler 1959); *Pr. hypnorum* (Postner 1952); *Al. alpinus*, *arcticus*, *balleatus*, *Ml. lapidarius*, *Pr. jonellus*, *lapponicus*, *pratorum* (Løken 1973); *Pr. jonellus*, *pratorum* (Alford 1975).

Some group specificities are suggested in these records. *Bombus* and, less consistently, *Megabombus* are principally underground nesters, *Thoracobombus* (= carder bees by Sladen 1912) are mostly surface nesters, and some European species of *Pyrobombus* are plastic as to site preference.

However, even in the species with rather fixed preferences, the tendencies seem not absolute. Based on the choice for artificial nest boxes placed on or below the ground, Hobbs (1964b~1968) obtained the following tendencies in the Alberta species: Surface > Underground *Fv. californicus*, *Pr. mixtus*; S ≈ U *Cl.*

rufocinctus, *Pr. flavifrons*, *frigidus*, *sylvicola*; S<U *Bb. nevadensis*, *Bo. occidentalis*, *Pr. bifarius*, *huntii*. Hobbs (1965a) indicates the difficulty of determining specific differences in nest site preferences. He says that specific differences in searching behavior between surface and underground nesters are unknown. In any event, it is never certain whether nesting in one type of box represents a real choice, preceded by the rejection of the other type. His cautious approach is certainly wise. But Jordan (1936a) recorded a difference in searching behavior of post-hibernation queens. Searching flight in some underground nesters is low (*Bo. terrestris*, *Ml. alticola*, *lapidarius*) while that of surface nesters is high (*Mg. hortorum*, *Th. humilis*, *muscorum*), though inclusion of *Mg. hortorum* in surface nesters is contrary to some records cited above. Anyhow, the above citation shows the occurrence of some species or group specificities in nest site preferences. According to Free and Butler (1959) the canal leading to underground nest cavities is long in *Bo. terrestris* and *Ml. lapidarius*, short in *Mg. hortorum*. Sladen (1912) and Alford (1975) write that the canal is longer in *Bo. terrestris* than in *lucorum*.

Postner (1952) discussed the relation between habitat and nest site preferences and suggested a closer relation between hylophilous (cf. 1) and surface nesting tendencies, probably due to the accumulation of nesting material on the forest floor. But he classified some underground nesters (e.g. *Bo. lucorum*, *Mg. hortorum*) as hylophilous and those without distinct underground preference as eremophilous (Cf. *confusus*, *Th. sylvarum*).

More precise results are presented by K.W. Richards (1975), who recorded the number of artificial nests used by some Alberta species (U=underground, FU=False underground, S=Surface, A=Above ground):

	U	FU	S	A	Total
<i>Bo. occidentalis</i>	64	9	10	5	88
<i>Pr. ternarius</i>	8	4	2	1	15
<i>bifarius</i>	61	21	16	11	109
<i>flavifrons</i>	18	9	1	4	32
<i>frigidus</i>	24	15	20	61	120
<i>Sb. appositus</i>	13	16	39	31	99
<i>Cl. rufocinctus</i>	11	25	34	40	110
<i>Fv. californicus</i>	6	16	20	17	59
<i>Pr. mixtus</i>	0	5	29	33	67

The results coincide well with those obtained by Hobbs. Use of above ground artificial nests is more frequent than in previous records. Richards argues that nest densities of above ground and underground nesters are respectively affected by the abundance of abandoned nests of birds and rodents. On the basis of three findings, scarcity of natural nests discovered, lasting site searching exhibited by post hibernation queens and frequent usurpations (cf. 28), he suggested the availability of nest sites as an important factor limiting nest density and causing intra- and interspecific competitions.

3. Nest entrance camouflage

Bumblebees do not prepare elaborate nest entrances as do many stingless bees. In some underground nesters, however, plant material is occasionally piled up around the surface entrance of the nest canal: *Rh. elegans*, *pomorum* (Hoffer, ref. Weyrauch 1934), *Fv. fervidus* (Plath 1934), *Bo. lucorum* (Free and Butler 1959, Alford 1975), *Bo. occidentalis*, *Fv. californicus*, *fervidus*, *Pr. bifarius*, *flavifrons*, *frigidus*, *huntii* (Hobbs 1964b~'68). Hobbs (1967) suggested the possible occurrence of two different tendencies: *Fv. fervidus* (Plath 1934) carries the material into the underground cavity and the excess is piled up around the nest canal entrance. On the other hand, in *Bo. occidentalis*, *Pr. bifarius*, *flavifrons* and *huntii*, the material is accumulated at the entrance before the arrangement of nest material. It is possible that this trait is more easily released in some species, but no quantitative data are available.

This piling of plant material has been called false nest or pseudonest. K.W. Richards (1975) called it tunnel camouflage, and showed its frequent performance in early emerging and predominantly underground nesting species, such as *Bo. occidentalis*, *Pr. bifarius*, *flavifrons* than in later emerging species with plastic site preference, e.g. *Cl. rufocinctus* and *Sb. appositus*. In the first mentioned species the piling is observed in the later season, too. Richards assumed this habit as a protection against flooding as well enemies and usurpers.

4. Aggressiveness

It is well known that aggressiveness of social insects increases with colony size and varies, as is familiar to beekeepers, with weather and food conditions. Nevertheless, various species of the same taxonomic group often differ remarkably in their manifestation of aggressiveness (in winged Hymenoptera, e.g. *Vespa*, Matsuura and Sakagami 1973; polybiine wasps, Richards and Richards 1951; stingless bees, Michener 1961, Kerr et al. 1967).

Sladen (1912) wrote that pollen storers (cf. 12) are more aggressive than pocket makers, but Plath (1934) criticized this opinion, regarding many Nearctic pollen storers as gentle. Some references on aggressive species: *Bo. terrestris* (Sladen 1912, Free and Butler 1959), *Fv. fervidus*, *pennsylvanicus*, *Pr. bimaculatus* (Plath 1934), *Bo. lucorum* (Free and Butler, 1959, though milder than *Bo. terrestris*, Løken 1961), *Fv. fervidus* (Stephen et al. 1969, *Sp. morrisoni* cited as passive), *Fv. atratus* (Sakagami, Akahira and Zucchi 1967). I have a vivid impression of *Fv. atratus*, which is incomparably more ferocious and ready to attack than the Japanese species. Because of this temperament most nests of *Fv. atratus* are burnt by Brazilian farmers as soon as discovered. According to Dias (pers. com.), *Fv. transversalis*, the unique bumblebee adapted to the tropical rain forest, is more ferocious than *Fv. atratus*. Aggressiveness seems to vary among consubgeneric species. *Bo. lucorum* is milder than *Bo. terrestris* (op. cit.); *Th. humilis*, *pascuorum* and *ruderarius* are mild but *Th. muscorum* is pugnacious (Alford 1975).

Aggressiveness is an ambiguous term involving some subjective judgements. First, intranidal aggression must be sharply distinguished from that against enemies. Queens are dominant but do not participate in nest defense. Secondly aggressiveness is often exaggerated by the pain received. Thirdly the intensity and persistence of attack are intimately linked with one another but can be separated. Some specifications devised for stingless bees (op. cit.) may be suggestive. Finally the tactics of attack may vary qualitatively as in stingless bees: Plath (1934) observed *Fv. fervidus* regurgitating honey when attacked. The same behavior is suggested for *Sb. appositus* (Hobbs 1966a, b). According to Sladen (1912) both *Bo. terrestris* and *Th. muscorum* are aggressive but the first species attacks the lower half of the disturber and does not pursue much, while the second species circles around the head of the disturber with persistent pursuit.

5. Preparation of the first brood cell

Until recently two controversial opinions have been cited on the first brood cell made solitarily by the founding queen: 1) First the wax cell is built, then pollen is deposited and the cell is closed after oviposition (Hoffer ref. Weyrauch 1934, Wagner 1907). 2) First the pollen lump is prepared, then eggs are laid in or on it and finally it receives the wax cover (Sladen 1912). The recent studies by Alford (1970) and Hobbs (1964a~'68) have revealed the validity of the latter opinion. At the same time Hobbs clarified that the preparation of the first cell is quite different from that of the second and subsequent cells (cf. 8, 9). The findings common to observations by the two authors are: 1) First, preparation of pollen lump, 2) then, deposition of several eggs on it, and 3) closure of the cell with wax¹⁾. On the other hand, some specific differences, possibly involving controversies of observations, are reported as follows.

5. 1. *Shape of pollen lump*: The shape is different among species (Alford): *Th. humilis*, *pascuorum*, square seen from above and pyramidal seen laterally, with rounded corners and slightly concave edges; *Pr. pratorum*, similar but slightly elongate, cushion form; *Mg. hortorum*, trapezoidal with shorter edge facing the nest entrance, longer edge concave and lateral edges convex, often shiny.

5. 2. *Position of eggs*: All vertical according to Alford and Hobbs, but Sladen (1912) recorded as horizontal in *Ml. lapidarius*. Stephen et al. (1969) described an egg laid horizontally in a single cell of *Sp. morrisoni*, but their illustration is drawn as if the cell is built on an older cocoon.

5. 3. *Location of eggs in or on the pollen lump*: First a terminological remark is necessary. Hobbs called the area of the pollen lump occupied by each egg a cell. Here adopting the usage by Michener (1974), the whole pollen lump receiving

1) The wax used for construction by bumblebees is dark because of an admixture of pollen. Henceforth it is simply called "wax".

egg and a wax canopy is called the first cell. The area corresponding to the cell as defined by Hobbs could be termed the subcell, if necessary, in order to maintain the unitary usage for the first and subsequent cells, both characterized by the abandonment of the unit-cell system and adoption of a distensible cell wall, by which bumblebees are unique among all Aculeata. In all subgenera observed by Hobbs except *Alpinobombus*, eggs are isolately laid each in a subcell. Only in *Al. balteatus* the eggs are laid jointly in the cell. The same habit was observed in *Al. polaris* (K.W. Richards 1973). Hobbs assumed it as an adaptation to the severe climate and K.W. Richards stressed it. As to the European species, Alford (1970) recorded oviposition on the pollen lump in *Th. humilis*, *pascuorum* and *Pr. pratorum*, but each egg laid in pollen surrounded with pollen walls in *Mg. hortorum*. As the species exhibiting the latter type he cited *Mg. ruderatus* (Sladen 1912), *Fv. pennsylvanicus* (Rau 1941) and some species observed by Hobbs. Later Alford (1975) writes that most species may adopt the latter type but *Thoracobombus* and *Al. balteatus* (Hobbs 1964b) the former type. If this opinion is true, the joint oviposition by *Thoracobombus* must be explained differently from that by *Alpinobombus* (cf. above). It is possible that there is some subtle difference between these two subgenera. The joint oviposition in *Pr. pratorum*, observed once by Alford, should also be restudied, together with oviposition types of many other subgenera.

5. 4. *Number of immatures in the first cell:* The number of immatures in the first cell is recorded in some species:

Al. balteatus mean 11 eggs (7~21), m. 14 larvae (12~15); *Bb. nevadensis* m. 12.4 larvae (8+additional 4); *Fv. californicus*, *fervidus* m. 10 and 8 pupae respectively; *Bo. occidentalis* 8.6±0.5 eggs with 1~2 additional ovipositions; *Pyrobombus* spp. mostly 8~9 pupae; *Sb. appositus* m. 13±3 pupae; *Sb. borealis*, for some queens 24 pupae (Hobbs 1964b-1968); *Mg. hortorum* 8~16 eggs or larvae; *Pr. pratorum*, *Th. humilis*, *pascuorum* 5~8 eggs or larvae. Mean numbers that emerge *Bo. lucorum* 12, *Mg. hortorum* 9.4, *Pr. pratorum* 7.0, *Th. humilis* 7.0, *pascuorum* 6.8, *ruderarius* 7.5 (Alford 1970); *Al. polaris* 16.2 eggs, 15.9 larvae (K.W. Richards 1973); Number of eggs *Bo. occidentalis*, *Pr. bifarius*, *flavifrons*, *frigidus*, *mixtus*, *ternarius* 8.20~8.95; *Cl. rufocinctus*, *Fv. californicus* 9.16~9.91; *Sb. appositus* 13.55~13.93 (K.W. Richards 1975).

Hobbs stressed the large mean numbers in *Subterraneobombus*. K.W. Richards is of the same opinion for the later emerging species (*Cl. rufocinctus*, *Sb. appositus*). The first cell of *Sb. subterraneus* also contains many immatures (Alford 1975). K.W. Richards (1975) explained the mean egg numbers, being equal to eight or more, by the production of at least one egg by each of eight ovarioles.

5. 5. *Sequence of ovipositions in the first cell:* Weyrauch (1934) denied sequential ovipositions in the first cell recorded by Hoffer. The recent observations by Hobbs favor the occurrence of sequential ovipositions. But his results suggest two different types of sequence. The oviposition process consists of the preparation of a subcell (*S*) and oviposition in it (*O*). Two subprocesses usually go

in sequence, e.g. *SO, SO, . .* or $n(SO)$. In some species, however, several subcells are built before ovipositions, *S,S,S. . . .*, then *O,O,O. . . .*, or nS, nO ($n=2$ in *Bb. nevadensis* and up to 4 in *Cl. rufocinctus* and *Pyrobombus* spp.). Alford also records the same tendency in some British species. Besides this sequence, Hobbs mentions additional ovipositions in some species, e.g. 8+4 additional eggs in *Bb. nevadensis* and 8+1~2 in *Bo. occidentalis* and some *Pyrobombus*. Such additional ovipositions are also recorded in *Sb. subterraneus* (Alford 1975), *Al. polaris* (K.W. Richards 1973) but not in *Al. balteatus* (Hobbs 1964b). In *Mg. ruderatus* and *Th. pascuorum*, too, the first cells receiving some eggs remain half-closed until additional eggs are laid (Alford 1970). K.W. Richards (pers. comm.) regards later additions as an outcome of delayed egg production by some ovarioles, after all eight ovarioles produced each one egg.

5. 6. Arrangement of eggs in the first cell: Arrangement of eggs in *Pyrobombus* is generally two eggs at the center and three on each side, forming three rows (Hobbs 1967). A similar tendency is recorded in *Pr. pratorum*, *Th. humilis* and *pascuorum*, but lateral rows become irregular at larger clutch sizes. The arrangement is more irregular in *Mg. horotrum* (Alford 1970).

5. 7. Differences between natural and artificial nests: Alford (1970) described noteworthy differences between the first brood cell built under natural and under artificial conditions. In artificial nest boxes, all queens of *Bo. lucorum*, *terrestris*, *Mg. hortorum*, *Pr. pratorum* and *Th. pascuorum* laid eggs horizontally. Instead of a pollen lump, a wax cell was built above the pollen mass or on the nest floor. The first cell made by *Th. pascuorum* in a nest box was similar to the subsequent ones. Probably the lack of some appropriate releasers, such as may exist in the nature of the nest substrate, etc., is responsible for this anomaly. Previous controversies may partly be explained in the same way. Some irregularities of nest structure evoked in nest boxes, e.g. in polygynic colonies artificially formed by Röseler (1965, mainly with *Bo. terrestris* and *lucorum*), might relate to the same factor.

6. Additional provisions for the first cell

Eggs laid on the pollen lump of the first cell receive a common wax canopy, which is rather transparent in *Cl. rufocinctus* compared with other species (Hobbs 1965b). After hatching and some growth, the larvae receive additional food. Some controversies concern this additional feeding, and relate to the presence or absence of feeding pockets beside later brood cells (cf. 12).

Hobbs (1964b) said for *Al. balteatus*: "First brood larvae were fed pollen through gaps in the canopies of both ends of the brood mass until they reach the last instar." He regards this manner as common to all subgenera observed by him, with the exception of *Bombias*. This seems common to all subgenera in the case of later cells, but definite confirmation is still required for many species.

According to Hobbs (1965a), only *Bb. nevadensis* inserts pollen through pockets

made at the both ends of the first brood cell, as practiced by the pocket making species for the subsequent cells (cf. 12). On the other hand, K.W. Richards (1973) writes of *Al. polaris*: "Egg cells have a definite area under them for fresh moist pollen during larval development. Thus the queen at this stage is a *pocket maker*." Alford (1970), writing about *Th. humilis* and *pascuorum*, says "pollen pockets were developed laterally beneath each larval clump, and the larvae fed upon the pollen mass, enclosed by the wax-pollen envelope which covered the top of the clump." Weyrauch (1934) also recorded the presence of feeding pockets beside first cells. The species were not mentioned but his studies were made mainly with *Th. humilis*, *pascuorum* and *runderarius*. The controversy depends on whether only *Bb. nevadensis* possesses the permanently opened pockets while other species or subgenera close the orifices soon after feeding.

Reaching the final instar, the larvae separate themselves "from each other by spinning flimsy, incomplete cocoons. They were then fed individually with a mixture of honey and pollen" (Hobbs 1964, *Alpinobombus*, but common to all other subgenera). The same trait is recorded by K.W. Richards (1973) in *Al. polaris*.

Although still much must be clarified, the first brood cell of bumblebees presents interesting differences from the subsequent cells as summarized below, together with the features found in the brood cells of three other tribes of Apidae.

Character	Bombini		Euglossini	Apini	Meliponini
	First cells	Later cells			
Number of eggs laid	Several		One		
Position of egg in cell	Vertical	Horizontal	Vertical		
Arrangement of eggs	Isolated (Compact in <i>Alpinobombus</i> and <i>Thoracobombus</i>)	Compact			
Provisioning	<i>Pollen</i> : Mass, even in pollen storers. <i>Honey</i> : Progressive	<i>Pollen</i> : Progressive in pollen storers, mass in pocket makers. <i>Honey</i> : Progressive	Mass	Progressive	Mass
Cell wall	Distensible		Fixed		
Removal of cell wall after cocoon spinning	Present		Absent	Absent	Present

The differences between first and subsequent cells probably depend on different nest substrates and social conditions. In the polygynic phase of *Fv. atratus* (cf. 27), the first cell made by each new queen does not differ from the subsequent ones (observed by me in the colonies artificially reared by Dr. R. Zucchi), but when solitary queens establish nests, the first cell is similar to that of the temperate congeners (Sakagami, Laroca and Moure 1967, Fig. 2 b, cited as a piece of wax, but indubitably it was the first brood cell). Likewise the first honey pot made by the solitary queen was like those of temperate congeners (cf. 7).

7. Honey pot prepared by the founding queen

Before or after the preparation of the first brood cell, the founding queen builds a honey pot near the nest entrance, separated from the brood cell. Although not confirmed in many species specifically, this seems to be a generic character¹. Only Weyrauch (1934) mentioned its differences from the pots later built by workers; paler with less admixture of pollen, more spherical than cylindrical, with the bottom less pointed. According to Alford (1975) the pots of *Pr. pratorum* are light colored, while those of *Mg. hortorum*, *Th. pascuorum* and many other species are yellowish or brownish. Plath (1934) reports a double pot built by a queen of *Sp. griseocollis*.

Sladen (1912) reported preparation of the first brood cell prior to the pot. Hobbs (1965a~1968) confirmed the same trait except for *Al. balteatus* (1964b) which made the pot first. For *Al. polaris* K.W. Richards (1973) reported preparation of the cell before the pot and the deposition of honey on moss or on the cotton bottoms of artificial nest boxes. Alford (1970) agreed with Sladen as to *Mg. hortorum*, *Pr. pratorum*, *Th. humilis* and *pascuorum*. In *Th. pascuorum* pots were never made before oviposition, but in a nest of *Mg. hortorum* the pot was made after the cell but before oviposition. Weyrauch (1934) writes that only one pot is built by the queen, but Wagner (1907) records several pots made by the queen. Additional pots may be made in some species, up to three in *Bb. nevadensis* (Hobbs 1965a) and 2~3 in *Al. polaris* (K.W. Richards 1973).

8. Location and clutch size of cells built upon the first cell

In contrast to the first cell, the next cells are built on the first cell (=the second brood by Hobbs and K.W. Richards). Hobbs confirmed for all subgenera observed by him that the cells built on the first cell were made upon the ridges formed along the sides of the median incubation groove. In most subgenera several contiguous cells are built upon one ridge and receive a common wax canopy so that the distinction between cells becomes difficult externally. The other ridge is employed after one ridge is covered with cells, but occasionally receives cells before the first ridge is completely used. In *Subterraneobombus*, however, the cells are, though occasionally clumped, usually built separately on or between the summits of the first cell, probably because the incubation groove is inconspicuous due to large clutch size (cf. 5. 4.). Similar separate cell building is also recorded in *Bv. nevadensis* which also has an inconspicuous incubation groove.

Richards (1973) also recorded for *Al. polaris* successive cell building on ridges. Usually one ridge is completely covered with egg cells before any are built on the other. But a cell is added only after the hatching of eggs in the cell made pre-

1) Here the term "generic" is used straightforward in the sense "common to all congeneric species," not in the particular sense used by Haas (1962~'66) as "generic behavior" (cf. Discussions).

viously¹⁾, so that each ridge is occupied by cells of different stages. He did not find the common wax canopy described by Hobbs (1964b) in *Al. balteatus*.

These cells built upon the first cell each contain only one egg in *Bb. nevadensis*, several eggs in other subgenera observed by Hobbs (1964b~1968): *Al. balteatus* 10, *Bombus* 4.2, *Cl. rufocinctus* 4.2 ± 1.2 , *Fv. californicus* 2~7, *fervidus* 3~4, *Pyrobombus* 3~4, *Sb. appositus* 3.6 ± 1.2 .

Unlike cells made later, the cells built on the first cell are usually contiguous. When these cells later distend and each larva begins to spin its cocoon, the cocoons belonging to one batch²⁾ are not always clearly distinguishable from those of adjacent batches, unless examined periodically as done by Hobbs and K.W. Richards (pers. comm.). This difficulty is well known in the later batches of some subgenera, especially *Bombus* s. str. (cf. 13), but must be particularly great in the case of the contiguous cells built upon the first cell. Many bumblebee nests are often discovered after reaching a fairly large size, i.e. when the earliest cocoons are sunk in the bottom of the nest cavity, already half-torn and dislocated. In such circumstances the actual size of earlier batches may occasionally be misestimated, especially when the batch size is small as in *Pyrobombus*. This point must be kept in mind when tracing the colony development by means of counts of batches of cocoons.

9. Location of the later cells

As the colony develops, egg cells are successively built upon older cocoons. The terms first, second and subsequent broods are frequently used (Hobbs 1964b~1968, K.W. Richards 1973). According to K.W. Richards (pers. comm.) the first brood is that laid in the first cell, the second brood is that laid in the cells made on the first cell, and subsequent broods are those laid later. This section deals with the last mentioned broods. The following citations mainly concern the cells usually isolated on the tops of older cocoons in well developed nests. Some specific differences are recorded:

Th. humilis, *pascuorum*, *ruferarius*, cells flat, built at niches between cocoons; *Ml. lapidarius*, cells tall, built on tops of cocoons. In no species are cells constructed on larval cells (Weyrauch 1934); *Th. pascuorum*, built on the cocoons with young pupae (Brian 1953); *Fv. atratus*, on tops of cocoons with young pupae or with spinning larvae (Sakagami, Akahira and Zucchi 1967); *Dv. diversus*, as in *Fv. atratus*, usually one cell per cocoon, if two, separated from each other (Katayama 1965); *Bo. ignitus*, *hypocrita*, only on tops of cocoons after, never before, completion of spinning, often two or more cells in contact or even fused on the same cocoon (Katayama 1967, 1971).

Wagner (1907, *Bo. terrestris*) and Løken (1961a, *Bo. lucorum*) also recorded many cells in contact on the same cocoon, but some of these cells might be built by

1) The cells made on the first cells, not the first cell itself.

2) The term "batch" is applied to the group of immatures born in the same cell. After cocoon spinning the demarcation of batches occasionally becomes difficult.

laying workers. The irregularity of such worker built cells in *Bo. ignitus* and *hypocrita* was mentioned by Katayama (1967, 1971). The following cases are also likely to be worker built cells (cf. 10): One egg cell above another (Weyrauch 1934, *Ml. lapidarius*; Sakagami, Akahira and Zucchi 1967, *Fv. atratus*), egg cell on the floor of the nest box (op. cit., *Fv. atratus*); numerous eggs in pollen cylinder (Hobbs 1967, *Pr. huntii*). As an extreme case, Haas (1965) recorded for *Ml. lapidarius* (? , not distinctly specified) that the wax cover and brood area were connected by means of pillars consisting of a series of abnormal egg cells which were not cared for by workers. He interpreted this as a secondary modification of egg cells into pillars.

10. Position of, and number of eggs in the later cells

For all observed subgenera Hobbs (1964b~1968) confirmed that eggs are laid horizontally in the second and subsequent cells, contrasting to the vertical orientation in the first cell (cf. 5. 2.). The same is a rule in *Fv. atratus* (Sakagami, Akahira and Zucchi 1967), *Dv. diversus*, *Bo. ignitus*, *hypocrita* (Katayama 1965, '71, '74) and probably in all other species. Erect orientation in the later cells was recorded in *Bo. terrestris* (Wagner 1907) and *Ml. lapidarius* (Weyrauch 1934). Wagner (1907) also showed an irregular orientation in *Bo. terrestris*. But Katayama (1971, '74) mentioned irregular orientation of eggs in worker built cells of *Bo. ignitus* and *hypocrita*, as is familiar in laying workers of honeybees. Such eggs of *Bo. lucorum* were also found in an orphan nest (Løken 1961a). The afore-mentioned cases of the eggs not laid horizontally may be attributed to the same cause.

The number of eggs laid in the later cells depends on colony conditions. Some precise records are available for *Dv. diversus*, *Bo. ignitus* and *hypocrita* (Katayama op. cit.). Weyrauch (1934) gives the range 2~40, mostly 8~13. The latter figures may be valid for the queen built cells of most species. The cells with unusually few or many eggs are likely to be worker built, as workers often remove eggs from, or add them to, the cells already containing eggs (Cumber 1949).

The only exception to the rule mentioned is in *Bombias*, the later cells of which are always single-egged (*Bb. auricomus*, Frison 1918 ref. Hobbs 1965a; *Bb. nevadensis*, Hobbs 1965a), nevertheless an allied subgenus *Separatobombus* deposits several eggs in each cell as in other subgenera (*Sp. griseocollis*, Plath 1927). Hobbs considered *Bombias* as the most evolved group of bumblebees (cf. Discussions).

11. Pollen priming in the later cells

In many species the second and subsequent cells do not receive food deposits before oviposition. Only some recent studies are cited: 'Most subgenera studied by Hobbs (1964b~1968); *Fv. atratus* (Sakagami, Akahira and Zucchi 1967); *Dv. diversus*, *Bo. ignitus* and *hypocrita* (Katayama, cf. 10); *Al. polaris* (K.W. Richards 1973). However, it has also been noted that some species prime the cell bottom with pollen. Sladen (1912) cited as *pollen primers* *Mg. ruderatus*, *hortorum*, *Sb.*

subterraneus and probably *Sb. distinguendus*. Other records are: *Pr. impatiens* (Plath 1934); some pocket makers and *Pr. pratorum* (Free and Butler 1959); *Pyrobombus* spp. usually if not always, *Sb. appositus*, *borealis* (Hobbs 1966b, '67); *Ag. wurfleini* (Løken 1973). It is noteworthy that this habit is recorded in *Subterraneobombus* and *Pyrobombus* from both hemispheres. Hobbs (1964a) regarded this habit as primitive (cf. Discussions).

Some related records are as follows: Wagner (1907) illustrated an egg cell of *Bo. terrestris* containing a pollen mass above the vertically laid eggs. Hobbs (1967) noted eggs of *Al. balteatus*, *Bo. occidentalis*, *Pr. bifarius*, *flavifrons*, *frigidus*, *huntii*, *sylvicola* sometimes being lined with a droplet of honey and of *Pr. bifarius* occasionally wax-lined. On the contrary Løken (1961a) recorded some cells of *Bo. lucorum* without bottoms, eggs lying directly on the substrate cocoon.

12. Pocket makers versus non-pocket makers (=pollen storers)

There are some controversies and ambiguities on this classification, which is apparently one of the most important bionomic grouping of bumblebees. First Sladen (1912) grouped pollen primers (cf. 11) and carder bees (Cf. 2) as *pouch makers* and some other species (*Bo. lucorum*, *terrestris*, *Cl. cullumanus*, *Kl. soroensis*, *Ml. lapidarius*, *Pr. jonellus*, *pratorum*, *lapponicus*) as *pollen storers*. Plath (1934) confirmed the validity of this classification for the Nearctic species. Considering the name pollen storers as inadequate, because pocket makers also deposit pollen outside of pocket (cf. 16), he proposed the names *Marsipopea* and *Amarsipopea*. Certainly these names, or simply pocket makers and non-pocket makers, are more appropriate and will be used below.

12. 1. General accounts of the two groups: Except for the first cell, pollen is fed to the larvae through the pocket made at the side of the larval cell in pocket makers, whereas it is given directly by perforating the cell wall in non-pocket makers. In both groups the honey is given directly through the cell wall. Hobbs (1964a~1968) confirmed in all subgenera observed by him that the last instar larvae were fed by a regurgitated mixture of honey and pollen after they separated themselves from each other with flimsy silken nets.

Concerning the first brood cell, the larvae receive additional pollen through the gaps in the canopies of both ends of the cells in all subgenera so far observed. This resembles the feeding by means of pockets. But the gaps are soon closed after feeding except *Bb. nevadensis*. In this species the pocket for the first cell is constantly open (cf. 6); nevertheless this species behaves as a non-pocket maker for the later cells (Hobbs 1965a).

12. 2. Relation between taxonomic and bionomic divisions: The subgenera involving the confirmed pocket making species are *Alpigenobombus*, *Alpinobombus*, *Diversobombus*, *Fervidobombus*, *Megabombus*, *Rhodobombus*, *Subterraneobombus* and *Thoracobombus*. The species with which the formation of pockets were definitely

recorded are difficult to enumerate, for the old papers often do not cite the specific names. But the absence of pockets has been reported definitely in no species belonging to the above mentioned subgenera. And all these subgenera except for *Alpinobombus* and *Alpigenobombus* belong to the Section *Odontobombus* defined morphologically, which implies a phyletic stability of this bionomic character. The subgenera, from which only non-pocket makers are recorded are *Bombias*, *Bombus*, *Cullumanobombus*, *Kalobombus*, *Melanobombus*, *Pyrobombus* and *Separatobombus*. As a rare exception, Løken (1973) mentioned this character for each species in Scandinavia as far as confirmed. Pocket makers, *Ag. wurfleini*, *Al. alpinus*, *arcticus*, *Mg. hortorum*, *Th. muscorum*, *pascuorum*; Nonpocket makers, *Bo. lucorum*, *magnus*, *terrestris*, *Kl. soroensis*, *Ml. lapidarius*, *Pr. jonellus*, *lapponicus*, *pratorum* (For *Alpinobombus* cf. 12. 4.).

12. 3. Feeding of sexual broods in pocket makers: In *Subterraneobombus* (Hobbs 1966b) and *Th. pascuorum* (Cumber 1949), all workers, male and queen larvae are fed through pockets. In *Dv. diversus*, the feeding to queen has not been observed but male and worker broods are fed through pockets (Katayama 1965) and some cells for queen larvae with pockets are illustrated (Morimoto et al. 1951, shown as "pollen bowls"). On the other hand, sexual broods of *Fv. fervidus*, *pennsylvanicus* (Plath 1934), *fervidus*, *californicus* (Hobbs 1966a), *Fv. transversalis* (Dias 1958, males not mentioned) are fed directly through cell walls. Recently Laroca (1972) found feeding pockets in a nest of *Fv. brasiliensis*, which involved new queens, and all pupae being sexuals. Zucchi (1973) recorded in *Fv. atratus* a condition intermediate between the two cases mentioned. In this species all castes are fed through pockets. But after the disappearance of the pocket, each queen larva, now individually separated, receives abundant regurgitated food through a continuously open orifice for 3~5 days (cf. 12. 7.). This orifice is also recorded in *Fv. transversalis*, but here the queen cells are not pocketed. These discrepancies indicate the necessity of closer comparative observations, including data on pockets in broods that are mixed as to caste or sex. Nothing is known as to the switch mechanism in such differential feeding.

12. 4. Observations on *Alpigenobombus* and *Alpinobombus*: All so far recorded pocket makers belong to *Odontobombus* except two subgenera cited below.

Alpigenobombus: Løken (1973) cites unpublished observations by Meidell on a nest of *Ag. wurfleini*: "One or two days after the larvae hatched, waxen pockets were built attached to the outer base of the batch. . . The broods were left alone during the first larval stages and were later fed by workers regurgitating pollen into their cells. The pollen was then often taken from the pollen pockets."

Alpinobombus: Løken (1961a) found a nest of *Al. arcticus*, which produced, excluding the first cell, at least two additional worker batches. One of them was yet a wax cell, containing eight larvae with a pocket. According to Hobbs (1964b), the second and subsequent broods of *Al. balteatus* produce sexuals, which are fed by direct regurgitation. Only in one colony were workers reared from the

second brood by feeding through pocket. K.W. Richards (1973) wrote on the second and third broods of *Al. polaris* as follows: "Fresh moist pollen is pushed into pollen pockets beneath the larvae on the edges of the brood when the first eggs hatch. The pollen pots for feeding males and queen larvae are larger than the pollen receptacles under the worker larvae. Bees at this stage of development become pollen storer." According to K.W. Richards (pers. comm) the superficial controversy between descriptions by Hobbs and Richards is explained by environmental conditions. In the years of milder weather conditions workers are seemingly produced in the second brood, which are fed through pockets. Løken (1973) recorded one nest of *Al. alpinus* and of *Al. balteatus* each. Both were at the sexual producing stage and the larval cells were not provided with pockets. She considered *Al. alpinus* as a pocket maker based upon "pollen bread stored beneath and adjacent to lower layers of masses of worker brood and, moreover, stuffed beneath some of the cocoons above." Her assumption may be correct, judging from the presence of pockets in other species cited above. But it may be premature to conclude so only from the facts mentioned above, because a similar case is recorded in *Pr. pratorum*, a non-pocket maker (cf. 16). She regarded both nests as already entered the "pollen storer" stage (cf. Hobbs, op. cit.). Summarizing, the larvae of *Alpinobombus* are seemingly fed as follows: The first batch (=the first brood, workers) and all sexuals fed by direct regurgitation, the workers occasionally produced in the second brood (=the second and subsequent batches) fed through pockets at early larval stages but by direct regurgitation at the final stage.

12. 5. Structure and ontogeny of feeding pockets: In *Fv. atratus* pockets increase in size with the growth of larvae and often more than one pocket is made per cell (Sakagami, Akahira and Zucchi 1967). In *Dv. diversus* the formation of more than one pocket is rather a rule (Katayama 1965). In *Fv. atratus* and *Dv. diversus* the orifices of pockets are distinctly directed upwards. This seems to be true for many other species, judging from the photographs by some authors. But the figure by Weyrauch (1934, *Th. ruderarius*) shows a rather oblique position and Wagner (1907) illustrated a pocket directing laterad or horizontally. It must be clarified whether such differences are specific or merely caused by spatial or colony conditions (cf. 12. 6.).

After pupation, pockets are destroyed in *Fv. atratus* and *Dv. diversus* (op. cit.). But the pocket is transformed to a pollen cylinder (=pollen pot) in *Fv. californicus* (Hobbs 1966a), though it is uncertain whether this happens obligatorily or facultatively. In *Cl. rufocinctus*, a non-pocket maker, a pollen pot is made at the side of the cell where pocket makers build pockets and is enlarged after cocoon spinning by larvae. Hobbs (1965b) regarded this as a condition intermediate between pocket makers and non-pocket makers (cf. Discussions).

Pockets are sometimes not built at proper position. In *Fv. atratus* a brood cell was made at the side of the pollen pot. After larval hatching the pot was trans-

formed into a pocket (Sakagami, Akahira and Zucchi 1967). A curious description was given by Weyrauch (1934) of *Th. pascuorum* and *ruderarius*. In these species a pocket disappeared after being used for 1~2 days by incorporation into the cell and another pocket was made. Weyrauch pointed out the importance of this process as it determines centrifugal expansion of the nest. Such succession was never observed in *Fv. atratus* and *Dv. diversus* (op. cit.) and no similar account has been reported for other species.

12. 6. Pocket in abnormal conditions: Descriptions given above suggest a behavioral plasticity or instability in some species. Two similar instances are cited from Haas (1962, 1965).

1) In the brood area of a small nest of *Pr. hypnorum*, a non-pocket maker, three empty cocoons were artificially filled with pollen. Probably because of this concentration of pollen pots near egg cells, which does not appear in the normal nest structure of non-pocket makers, four "pollen pockets" of the size of egg cells were prepared along the outer wall of an old pollen pot, though not communicating with the latter. The queen laid eggs in them, later opened them, devoured the eggs and filled one pocket with honey. Workers returning from the field deposited pollen in one of them. Later workers so modified the pot with abnormal pockets that it took on the appearance of a pollen pocket normally built by the pocket makers, attached to the egg cell, though the larvae were separated from pollen by the wax wall and fed directly through the cell wall, not through the "pocket." Haas interpreted this conflicting behavioral sequence as an unstable phenocopy of the behavior of pocket makers by a non-pocket maker, caused by a situation new for a non-pocket maker but similar to that usual in pocket makers. The transformation of a pollen pot into a pocket is recorded also in *Fv. atratus* (12.5.).

2) In some old larval cell of *Th. humilis*, the horizontally laid pockets are extended and directed vertically, reaching the level of the upper surface of the cell. But pollen is not deposited in them and larvae are fed directly, whereas horizontal pockets of younger cells still receive pollen. Haas regards such vertical pockets as functionless pollen pots and interpretes them as a morphological transformation (pocket→pot) not accompanied with corresponding behavior. He comments further: "In Zusammenhang mit dem in dieser Arbeit beschriebenen generischen Verhalten, zeigt das obige Beispiele, wie ein wichtiges generischen Element (nämlich der Pollentopf) in jeweils verschiedener arttypischer Bindung aufzutauschen kann und wie man in arttypischen Verhalten, wenn man es entwicklungs-geschichtlich bis in seine letzten Einzelheiten verfolgt, überall die generischen Verbindungslinien findet."

His *generic behavior* will be dealt with in Discussions, but the following remarks relate to the case; 1) Vertical and functional pockets are rather a rule in some other species (12. 5.). 2) The absence of pollen deposition in pockets of old cell may be normal, if the statement by Hobbs (1966a, b) is valid for all pocket makers (cf. 12. 1, 12. 7.). 3) Hobbs (1966a) reported the change of pollen pockets into pollen 'pots in *Fv. californicus*. Moreover, preparation of pollen pots is recorded for some other pocket makers, too (16).

12. 7. Feeding not through pockets: According to Hobbs (1964b~1967) the last instar larvae are fed by direct regurgitation even in the pocket makers observed

by him. This may be true for other pocket makers, but definite statements are absent for many species. In some pocket makers even earlier instar larvae are often fed by regurgitation (*Dv. diversus*, Katayama 1966; *Fv. atratus*, Sakagami, Akahira and Zucchi 1967) though this was not observed in *Dv. diversus* for the larvae earlier than three days old. Under artificially forced conditions, *Fv. fervidus* and *Sb. borealis* reared all larvae solely by regurgitation (Plowright and Jay 1968).

Detailed observations on the behavior sequence of the queen from pollen intake to regurgitation was described for *Bo. ignitus*, a non-pocket maker. A controversy exists as to feeding act. Wagner (1907) and Haas (1962) illustrated the extension of the glossa at feeding. Hobbs (1966a) also mentioned such behavior in *Fv. californicus*. But Meidell (1934, *Th. pascuorum*), Sakagami, Akahira and Zucchi (1967, *Fv. atratus*) and Katayama (1966, *Dv. diversus*; 1973, *Bo. ignitus*) did not observe such behavior. The glossa is not extended at feeding for larvae in the European honeybee (Lindauer 1952). In innumerable observations on food regurgitation between adult workers in honeybees and stingless bees, I have always confirmed the extension of the glossa by the recipient, never by the donor.

In *Fv. transversalis* and *atratus* each final instar larva of sexual broods is fed through a permanent orifice made in the still loose cocoon (cf. 12. 3.). In *Bo. ignitus* a similar permanent orifice for each larva is found even in the worker brood (Katayama 1973). In this species, however, the permanent orifice seems to relate to another bionomic character. Sladen (1912) mentioned the loose nature of the wax cover of the larval cell in *Bo. lucorum*, *terrestris* and *Sb. subterraneus*. The resulting orifice is usually thinly closed by larval silk but often remains unclosed. Plath (1934) noted the same trait in *Bo. affinis* and *terricola* and called *Bombus* s. str. bionomically *Phaneroschadonia* in contrast to *Cryptoschadonia*, which embraced in his definition all other groups of non-pocket makers (=Amarsipopea). The same tendency was also observed by Hobbs (1968, *Bo. occidentalis*, *terricola*). It must be questioned how a *positive* character, the permanent orifice, relates to a *negative* character, the loose wax cover. Plath (1934) suspected the loose wax cover of the larval cell of *Sb. subterraneus* reported by Sladen to be a result of hot days. But Hobbs (1966b) observed a similar tendency in *Sb. appositus* and *borealis*. It is open to further studies whether *Bombus* (non-pocket makers) and *Subterraneobombus* (pocket makers) developed the same trait independently or not.

13. Arrangement of cocoons forming a batch

Wagner (1907) described the cocoon arrangement of *Th. muscorum* as unilateral, i.e. all cocoons facing the same direction, that of *Ml. lapidarius* as bilateral to radial, though the cocoons of the sexuals of the latter species are arranged unilaterally. This character has not been mentioned by other authors. Another more often cited character is the compactness of the batch of cocoons. Sladen (1912) mentioned that the cocoons of *Th. humilis*, *pascuorum* and *sylvarum* are tightly fused to one another, those of *Ml. lapidarius* relatively compact and of *Bo.*

lucorum and *terrestris* very loose. Later this difference was generalized: Cocoons of pocket makers are compact but those of non-pocket makers are loose so that the batches are difficult to recognize (Free and Butler 1959, Løken 1961a). This difference seems valid to some degree, but does not exclude the difference among non-pocket makers. The loose connection of cocoons seems characteristic of *Bombus* s. str. (cf. 12. 7.), but it is uncertain whether other non-pocket makers, e.g. *Pyrobombus*, always form batches looser than do any pocket makers. No precise statement has so far been given as to the arrangement of cocoons in *Bombus*, the second and subsequent cells of which each receive only one egg (cf. 10) so that no batch exists in the sense defined in 8. Coloration of cocoons seems to some degree specific, e.g. pale yellow in *Ml. lapidarius* but deep yellow in *Th. ruderarius* (Alford 1975).

14. Arrangement of batches

Wagner (1907) distinguished several types of arrangements of batches, which were adopted by Weyrauch (1934) with slight modifications: I. Planloses Durcheinander der Einzelteile (*Bo. lucorum*, *terrestris*), II. Schichtenförmiges Nebeneinander der Wabenregionen gleicher Entwicklungsstufe ohne bestimmter Bauplan (*Ml. lapidarius*), III. Gekreuzte längliche Wabenplatten (*Th. humilis*, *ruderarius*), IV. Vogelnestartige Rosette (*Th. sylvarum*, *veteranus*), V. Kranzförmig um das Nestzentrum angeordnete Einzelrosetten (*Th. pascuorum*). According to Sladen (1912) the batches of *Th. humilis*, *sylvarum* and *pascuorum* often show a ring arrangement while those of *Ml. lapidarius* are at first compact but later irregular. After citing Wagner and Weyrauch, Alford (1975) gave the following additional comments: Combs of *Mg. hortorum*, *ruderatus* and *Sb. subterraneus* lack usually a definite structure, combs of the latter species being poorly organized. Little or no precise structure in *Bo. lucorum* and *terrestris*. Combs of *Ml. lapidarius* well arranged.

Specific or group differences in batch arrangement may exist but so far have been largely ignored. The arrangement may be less stable in; 1) non pocket makers than pocket makers, because of the absence of pockets, which may direct the arrangement of batches (Weyrauch 1934, Sakagami, Akahira and Zucchi 1967) and because of the loose arrangement of cocoons (13, 2) the species forming larger colonies because of the impossibility of maintaining definite arrangements. These comments seem valid for the species cited above. *Bo. terrestris* and *lucorum* (Type I) are non-pocket makers, forming large colonies; their cocoons are loosely arranged. *Ml. lapidarius* (II) is facultatively subterranean and the cocoons are fused less loosely than in *Bombus* (13). Type III~V are all carder bees (*Thoracobombus*), forming relatively small, surface and pocketed nests. It may be difficult to maintain an unoccupied nest center, as in the carder bees, in large underground nests, or in huge surface nests of some Neotropical species (Dias 1958, Zucchi 1973). On the other hand, the poor arrangements of *Megabombus* and *Subterraneobombus* (Alford 1975) do not favor the two comments mentioned, suggesting a group specificity

independent of colony size and presence or absence of pockets.

The types distinguished by Wagner and Weyrauch do not involve the species of *Pyrobombus*, the largest subgenus with flexible nest site preferences (2). Armbruster (1914) recorded a spiral arrangement in a nest of *Pr. pratorum*, but his illustration showed that the nest center was occupied by batches. A tendency to keep the nest center unoccupied occurs in the earlier batches built on the first cell (cf. 8), but it alone could not inhibit the occupation of the central area by enlarged cells. Weyrauch (1934) stressed the importance of the preparation of pockets at the sides of the cell to the whole nest arrangement (cf. 12. 5.). But he pointed out that this tendency alone was insufficient to maintain the unoccupied nest center and to explain the differences among types III~V. Although incorporation of old pockets was never seen, centrifugal expansion was noted in a small nest of *Fv. atratus* kept in an observation hive, mostly by translocation of substrate, but occasionally by direct translocation of cells (op. cit.). Anyhow, the distensible cell system of bumblebees must have evolved behavioral adjustments to avoid the collision of cells. Postner (1952) assumed that advanced types (III~V) evolved in parallel with surface nest foundation. But it is still open to question whether these types really represent more evolved patterns.

15. Honey storage

Honey is deposited either in empty cocoons or in wax pots. Many older cocoons near the nest bottom are torn and broken, but the cocoons of upper and intermediate layers are often used to store honey. Some cocoons are used without further elaboration for temporary deposition, but many cocoons receive wax collars and are sealed with wax lids when filled with honey.

Weyrauch (1934) mentioned the difference between honey pots built by the queen during the solitary brood rearing phase (cf. 7) and those built after the expansion of the nest. According to him the honey pots of the latter type are always built besides batches of cocoons, never above the cocoons containing pupae, and never beside cells with larvae. The honey pots are not numerous and usually are isolated from one another. Further, he recorded for *Bo. lucorum*, *terrestris* and *Mg. hortorum* the deposition of honey in small pockets built on the outer skirts of the wax nest envelope (cf. 17). This partial use of wax envelope for honey storage does not necessarily contradict the suggestion by Haas (1965), who asserted the derivation of the wax envelope through modification of honey pots at the nest entrance.

Free and Butler (1959) wrote that thin honey was stored in pots, dense honey in cocoons. K.W. Richards (1973) wrote for *Al. polaris* that cocoons were filled with honey up to one fourth of their capacity, and pots to one half to three fourths of their capacity. Apparently this is not a rule in some other species, whose cocoons receive lids after being filled with honey. Without specifying honey or pollen pots, Hobbs (1964a~1968) mentioned specific or subgeneric differences in

readiness to construct pots (*Cullumanobombus*, *Pyrobombus* > *Bombus* > *Subterraneobombus*) in relation to the capacity for wax production (cf. 18).

16. Pollen storage

Usually pollen is deposited in pots or cocoons. Weyrauch (1934), who gave the most precise information, distinguished the following kinds of receptacles: 1) Cocoons. Usually open. When rarely closed, the lid is flat, not convex as in those containing honey. 2) *Pollenbecher* (observed in *Th. humilis* and *rudericarius*). Always built alone, these are thin walled and flat bottomed as in queen built honey pots, but a little larger, as large as the cocoons of medium sized workers. They are at the side of larval cells, the upper margin lying at the level of the cell bottom. From the location and the thick margin of the orifice, incorporation into a larval cell is possible but so far not confirmed. 3) *Becher* without wax wall. Rarer. Later removal of wax wall? 4) *Pollentopf* (=pollen pot). Larger than *Becher* and becoming longer, these certainly correspond to the pollen cylinders of Sladen (1912). 5) *Pollentasche*. Comparable to honey pockets built on the lateral part of the wax envelope (cf. 15). 6) Amorphous pollen deposits. Pollen masses without wax cover, deposited in the interspaces among cocoons, or sometimes with a wax cover (*Pr. pratorum*, Bischoff 1927, p. 297). 7) *Pollennapf*. Pollen pockets built by pocket makers (cf. 12).

Among the types enumerated by Weyrauch, the distinction of *Becher* and *Topf* requires further studies with various species. Elongate pollen cylinders are known in *Bo. lucorum*, *terrestris* (Sladen 1912), *Bo. lucorum* (Løken 1961a), *Bo. affinis*, *terricola* (Plath 1934) and *Bo. occidentalis* (Hoobs 1968). Concentration of several pollen cylinders is known in *Bo. lucorum*, *terrestris* (Haas 1962), and some species of *Bombus* and *Pyrobombus* (Hobbs 1968).

Amorphous pollen deposits are also recorded in *Bombus* s. str. (Hobbs, and *Al. alpinus* (Løken 1973). In *Bb. nevadensis*, "the queens store pollen in mounts besides the cocoons on the peripheries of the first brood masses, though later stored in wax pots" (Hobbs 1965a). Similar deposits are made by *Sb. appositus* and *borealis*, but the clumps are often shiny and jelly like as if mixed with honey or other products of regurgitation (Hobbs 1966b).

Many pocket makers also build wax pollen pots in the absence of pollen pockets: *Fv. fervidus*, *pennsylvanicus* (Plath 1934), *Al. balteatus* (Hobbs 1964b), *Fv. californicus* (Hobbs 1966a), *Al. alpinus* (Løken 1973). According to Hoffer (cf. Weyrauch 1934) pollen cylinders of *Rd. pomorum* are very long. The amount of pollen deposited seems smaller in pocket makers. This is to be expected because pockets function as both pollen feeders and pollen receptacles. But except *Subterraneobombus* (Hobbs 1966b), no concrete data are available on whether pocket makers really and always build less pots than non-pocket makers.

If the opinion of Haas (1965) is correct, honey pots tend to be found more peripherally than pollen pots. Some records mentioned in 15 and 16 seem to justify this

statement. This also accords with the arrangement adopted by honeybees and, though less regularly, by stingless bees. Preparation of storage pots which are heteromorphous from brood cells is common to bumblebees and stingless bees. This suggests a parallel evolution than common descent. Use of the same type cells for both brood rearing and food storing in honeybees is possibly a secondary acquisition, when their ancestor adopted arboreal nests hanging from substrates. In this architectural plan, building of two different constructs, larger pots and smaller brood cells, is less adaptive than synchronous building of numerous repeatedly used cells.

17. Wax nest envelope

Bumblebee nests are always covered with an outer envelope consisting of plant matter. Many species prepare beneath this outer envelope a wax inner envelope, which covers the nest completely or partially. Specific differences in preparing this envelope have been pointed out by some authors:

Constant and complete in *Ml. lapidarius*, very frequent in underground nesters (*Bo. lucorum. terrestris*, *Mg. hortorum*, *ruderatus*), but rather rare in carder bees, especially nearly always absent in *Th. ruderarius* (Sladen 1912); Complete in *Ml. lapidarius* (Wagner 1907); Present or absent in *Bo. terrestris*, *Mg. argillaceus*, *Ml. lapidarius*, *Rd. elegans*, *Th. sylvarum*, absent in *Pr. pratorum* and *Th. ruderarius* (Bischoff 1927); Frequent in underground nesters (Free and Butler 1959); Frequent in *Al. balteatus*, *Bombias*, *Bombus* and *Cullumanobombus* (Hobbs op. cit.); Frequent in populous nests of *Bo. lucorum*, *terrestris* and *Ml. lapidarius* (Alford 1975).

The preparation of the wax envelope seems facultative, according to environmental and colony conditions. Wagner (1907) observed envelopes built by *Th. humilis* and *ruderarius* reared in artificial nests, both being carder bees which usually do not build envelope under natural conditions. Haas (1965) writes that most surface nesters build the wax envelope soon after emergence of the first workers, a statement contrary to previous records. He also notes that both underground and surface nesters prepare the wax envelope by removing the plant outer envelope and supplying wax. Many nests of *Fv. atratus*, a surface nester usually without wax envelope, build the envelope in winter, when reared in artificial nests (Zucchi unpub.). Probably most species possess an innate tendency to prepare the wax envelope, but the release of this trait seems variable among species, quick in some species such as *Ml. lapidarius* (2 days), slow in others, e.g. *Th. ruderarius* (1 week) (Weyrauch 1934).

The wax envelope apparently has homeostatic functions against adverse conditions such as enumerated by Weyrauch (1934), moisture (Hoffer), dessication (*Ml. lapidarius*, *Th. humilis*), cold (cf. also Hoffer, Haas 1965), dust (*Bo. lucorum*), and wind (*Ml. lapidarius*, *Th. humilis*). It is unknown which of these factors is most important.

In the species easily preparing the wax envelope, its lateral parts often consist of two to three sheets, where sometimes small pockets are formed, which

occasionally serve as food receptacles (cf. 15, 16). In *Bo. lucorum*, *terrestris* and *Ml. lapidarius*, Haas (1962, '65) recorded transformation of honey pots into the upper horizontal part of wax envelope. He regarded this as an instance of ethological allochory, e.g. the behavioral change caused by the differences of functional areals within the nest.

18. Wax production

Specific differences in wax production have been mentioned by some authors. Sladen (1912) noted poor wax production by carder bees. Weyrauch (1934) pointed out that rich wax production by *Ml. lapidarius* has unanimously been recorded by earlier authors. Concerning the species in Alberta, Hobbs (1964a~1968) gave the following order for wax production: *Cullumanobombus*, *Bombias* > *Pyrobombus* > *Fervidobombus* > *Bombus* > *Subterraneobombus*. K.W. Richards (pers. comm.) confirmed this order from his own observations with Alberta species. For the British species, Alford (1975) mentioned *Sb. subterraneus* and *Th. sylvarum* as poor wax producers. In honeybees, the Asiatic honeybee, *A. (Apis) cerana* ssp. is the excellent wax producer compared with its European cousin, *A. mellifera*. This trait is advantageous to build nests quickly after absconding which is frequent in *A. cerana* (Sakagami 1960).

Plath (1934) noted that the wax of *Bombus* s. str. is dark and brittle. Alford (1975) described the coloration of combs of some British species as follows: Dark brown (*Bo. terrestris*, *Pr. pratorum*, *Th. ruderarius*), darker than *Th. humilis* (*Th. muscorum*), darker than *Mg. hortorum* (*Th. ruderatus*), lighter than others (*Ml. lapidarius*), yellowish brown, often reddish (*Th. pascuorum*), yellowish (*Mg. hortorum*, *Th. humilis*). Such characteristics may in part but not totally affected by materials mixed into the wax. Group differences in the cerumen (wax mixed with resin, etc.) in stingless bees are well known. It ranges from semitransparent without admixture of resin in *Hypotrigona* s. lat. through pale in *Nannotrigona* and *Plebeia* to dark in *Scaptotrigona* and *Melipona*. The admixture of pollen in wax of bumblebees has been known for many years. The collection of resin, practiced by both honeybees and stingless bees, has so far not been recorded for bumblebees. Recently Laroca (1972) found an accumulation of human feces in the entrance canal of *Fv. brasiliensis*, a trait known in some stingless bees and in the genus *Eulaema* in the Euglossini (Zucchi et al. 1969).

19. Intranidal behavior

The complete behavior inventory of any bumblebee species has not been presented. Sakagami and Zucchi (1965) described most, if not all, of intranidal behavior patterns of *Fv. atratus*. Many of these may be common to other species and some must be characteristic of the genus, for instance, ejection of liquid excrement at nest periphery, raising of mid and hind legs of one side when mildly threatened, accompanied with the inclination of the body to the opposite side (cf. also

Plath 1934), and the feline-like upside down posture when severely threatened. At least no paper has recorded the lack of these postures. All these postures are absent in honeybees and stingless bees. On the other hand, food regurgitation between nest mates is frequent in honeybees and stingless bees, but has not been recorded in bumblebees except three instances (Verlaine 1934, Jordan 1936b, Khalifman 1953).

As a possible specific difference, Wagner (1907) notes that in nest repair *Th. muscorum* brings together the material from various directions with the legs, while *Bo. terrestris* carries each piece, one by one, with the mandibles. It is unknown whether this indicates a specific difference or merely reflects adjustment to different situations.

In all bumblebee species, the preparation of a brood cell and subsequent oviposition by the queen seem to proceed as a tightly linked behavioral sequence: Site selection - accumulation of material - cell building - oviposition - sealing - and nearly invariably honey intake. In *Fv. atratus* (Sakagami and Zucchi 1965) workers participated but little in this process. In *Bb. nevadensis* workers sometimes build cells in which the queen later lays eggs (Hobbs 1965a). In the preparation of the brood cells, the queens of *Dv. diversus* and *Bo. hypocrita* accepted help by workers to some degree (Katayama 1965, 1974), but the queen of *Bo. ignitus* worked solitarily (Katayama 1971). Sladen (1912, *Ml. lapidarius*) and Meidell (1934, *Th. pascuorum*) recorded the reopening of a cell once sealed, followed by additional ovipositions. Such behavior was not observed in *Fv. atratus*. In this species, the queen began to seal the cell without completing oviposition, when she was artificially removed from the laying posture. In this case, however, her behavior might change when separated from the cell for a longer time. Many, if not all, of these differences may depend on colony conditions rather than representing specific differences. A most needed study is precise comparative observations of queen behavior at the preparation of the first cell and oviposition in it (cf. 5).

20. Flower visiting habits

Certainly this section is the most incomplete part of the present review. Innumerable papers have been published on the flower visiting habits of bumblebees, not only from the purely scientific standpoint, but also in connection with crop pollination, in particular, that of legumes. Pittioni (1942a), Kugler (1943), Brian (1954), Free and Butler (1959) gave appropriate reviews of previous contributions. Thereafter, many interesting papers have appeared and the lists of preferred flowers have been published in various areas, e.g. Scandinavia (Løken 1973), England (Alford 1975), Alberta (K.W. Richards 1975), etc. Only a few aspects interesting from the comparative standpoints are referred to here. The papers on crop pollinations are found by consulting Free (1970).

Previous contributions show that bumblebees generally prefer relatively tubular flowers than in many other bees, e.g. honeybees, apparently for their long

tongues. Consequently, the lists of flowers visited by them cover only a part of all flower species available for all bees. Under this mild restriction, however, most species are polytrophic, visiting various flower species. This is easily understood from their eusocial life, which makes the strict oligotrophy impossible. A rare exception is *Mg. consobrinus*, which is strongly partial to *Aconitium*, and the distribution approximately coincides with the range of that plant (Løken 1961b). But in other species, too, the flower visitation spectrum varies often from species to species. This may depend in part on the tongue length. Long tongued subgenera such as *Megabombus*, *Subterraneobombus* and *Diversobombus* generally prefer tubular flowers, often showing a neat difference of flower choice from sympatric species of short tongued subgenera, e.g. *Bombus* and *Pyrobombus*. Nevertheless, the tongue length alone cannot explain the different flower preferences completely.

From observations under natural and experimental conditions, Brian (1957) specified the differences in foraging habits among four Scotch species relative to the following categories: I. Preferred habitat; II. Preferred flower type; III. Collecting behavior; IV. Reaction to other species; V. Season. The results are summarized as follows (not all categories are mentioned in some species):

Bo. lucorum: I. Exposed, adaptive to man-made environment; II. Open; III. Foraging honeydew, stealing nectar. Foraging pollen without taking nectar; IV. Indifferent; V. Long.

Mg. hortorum: II. Long tubular; III. "Psychologically" unadapted to stealing nectar and to pollen foraging without nectar intake. Tongue is extended at landing irrespective of the presence of nectar.

Pr. pratorum. I. Sheltered, II. Open; IV. Aggressive; V. Earlier.

Th. pascuorum: I. Sheltered; II. Medium, open in the absence of *Pr. pratorum*; IV. Timid; V. Later.

Based upon these results Brian assumed that preference is rather plastic, to some degree determined environmentally except for the tongue length, as already suggested by Pittioni (1942a) and Kugler (1943). K.W. Richards (1975) sought to measure how flower visits overlap among various bumblebee species in Alberta and showed some specific differences not always being determined by tongue length alone, though obviously not strictly innate as in many oligolectic bees. He explained the preferences as an outcome of food competition in the evolutionary course of the bee assemblage.

Nextly some more particular aspects of flower visiting habits are dealt with. Comparing *Bo. terrestris*, *Ml. lapidarius* and *Pr. hypnorum* in Sweden, Hassselrot (1960) stated that *Pr. hypnorum* began foraging earlier and ceased later for each day. Panfilov (1965) recorded the foraging period of three species in the environ of Moscow as follows: *Cf. confusus* 8~17:00, *Kl. soroensis* 6~20:00, *Ml. lapidarius* 5~7:00 and 19~20:00. K.W. Richards (1973) published detailed records of foraging activities by *Al. polaris* in high Arctic continuous daylight. K.W. Richards (1975) showed specific differences in daily foraging activities in Alberta species. The periods widely overlap among the species for both queens and

workers. Yet some distinctive patterns are recognized, e.g. *Fv. californicus*, *Sb. appositus* and workers of *Cl. rufocinctus* with a higher evening activity while queens of the last species with a higher morning activity than other species.

Concerning the time (min.) spent for each foraging trip, Free (1955b) obtained the following specific differences:

	Trip		Intertrip	
	Nectar	Pollen	Nectar	Pollen
<i>Th. sylvarum</i>	12.5	18.4	2.2	3.4
<i>pascuorum</i>	20.3	22.4	1.7	2.9
<i>Pr. pratorum</i>	20.0	33.3	1.9	2.7
<i>Bo. lucorum</i>	53.6	128.9	3.8	5.3

The mean number of trips per day (pollen and nectar combined) was 10.7 in *Th. sylvarum* but only 4.3 in *Bo. lucorum*. Free explained the lasting trips of *Bo. lucorum* by its large body size. It is interesting that *Th. sylvarum* works rapidly. Both Løken (1973) and Alford (1975) mention its "nimble flight and shrill hum". Alford (1975) notes the rapid flight and ease to be disturbed at foraging of *Sb. subterraneus*.

Concerning the flower constancy both Brian (1951a) and Free (1970a) report a tendency of *Bo. lucorum* to concentrate on fewer pollen sources than in *Th. pascuorum*. The percentage of mixed pollen loads was 34% in *Bo. lucorum* but 63% in *Th. pascuorum*, though in both species more frequent than in honeybees (6%). They suggest an attempted mobilization of the foraging force to work with a particular crop in *Bo. lucorum*, probably guided by the scent of predominant pollen source. If this is the case, a care must be taken not to confound the real oligotrophy such as expected in *Megabombus* and other long tongued subgenera and the superficial oligotrophy due to the concentration to a few food sources at a given time, which is also very conspicuous in honeybees (Sakagami and Fukuda 1973).

As to the relation between bumblebees and particular plant groups, the study by Macior (1970) on the pollination of seven *Pedicularis* species in Colorado Rocky Mts. is noteworthy. These plants are mostly pollinated by some of twelve bumblebee species. None of them are oligotrophic. Nevertheless, each flower species is characteristic in vertical distribution, phenology, flower size and nectar secretion, and pollinated by a set of particular species, sometimes of particular castes. This indicates that a plant group can adaptively radiate for a group of pollinator species, each of which is not oligotrophic. Probably this "unilateral" evolution can be applied to many instances of flower diversification without accompanied with specialized pollinators.

Another well known trait in bumblebees is nectar stealing, so far recorded in some species of *Bombus* (*affinis*, *terricola*, Plath 1934; *lucorum*, *terrestris*, Pittioni 1942, Kugler 1943, etc.; *hypocrita*, Sakagami 1951) and in *Ag. wurfleini* (Pittioni, Kugler, op. cit.). *Bombus* spp. mainly pierce the base of the corollar tube with stout maxillae, while *Ag. wurfleini* gnaws the corolla with highly differentiated

mandibles (Pittioni 1942a). With reference to the specific differences cited previously, Brian (1957) developed a hypothesis to explain the evolution of nectar stealing:

With inaccessibility to nectar the foragers first release random biting of floral tissues as a simple displacement reaction. But occasional success from this biting opened the way to the biting behavior as a specialized habit for nectar stealing. This biting is regarded as an aggressive behavior, and the readiness to bit the flower is higher in *Bo. lucorum* and *Pr. pratorum*, both being more aggressive than *Th. pascuorum* at nest defense. This hypothesis also explains deliberate pollen collection from incidental pollen collection. Biting and pulling at the stamens are regarded as a displacement reaction released when the stamens blocked the way to nectar. Pollen foraging not accompanied with nectar intake is more skillful in *Bo. lucorum* and *Pr. pratorum*, whose threshold of aggression is lower. The coadaptation of long tongue and tubular flowers was possibly achieved by those species which are "psychologically" unadaptive to obtain nectar by means of stealing, because it is doubtful whether the extra long tongue of *Mg. hortorum* and *Th. pascuorum* confers any advantage to the species over the short tongued congeners.

This hypothesis is instructive for the interpretation of nectar stealing. But some comments must be added: 1) As cited above, the species of *Bombus* s. str. frequently use maxillae instead of mandibles to steal from the flowers. To complete the picture, the origin of this behavior must also be explained. 2) Even if some species or subgenera are "psychologically" unadapted for nectar stealing, this could not be taken too seriously, because Kugler (1933) induced nectar stealing by piercing in *Th. pascuorum*. 3) It seems certain that species of *Pyrobombus* steal nectar far less frequently than *Bombus* s. str.; nevertheless *Pr. pratorum* is seemingly more aggressive than *Bo. lucorum* at flowers (cf. above). This suggests that the evolution of nectar stealing does not depend solely on the liberation of aggressiveness at flowers. The results by Brian indicate the necessity for closer comparative studies of foraging behavior in various subgenera, especially *Alpigenobombus* with peculiarly differentiated mandibles.

An interesting account is cited by Heinrich and Raven (1972) on nectar stealing. The elimination of nectar stealing species was proposed to increase seed production in red clover. But it has shown several times that an increased population of these stealers significantly increased seed production. Heinrich and Raven postulated that under conditioning of ample nectar secretion the actual pollinators (non-stealing long tongued bumblebees) visited more flowers when less nectar remained per flower after stealing. Their discussions on various relations of energetics and pollination ecology involve valuable suggestions for pollination problems, though not directly concern with the comparative standpoint.

Another interesting behavior is pollen collecting from tubular anthers of *Solanum* and *Cassia*. According to Michener (1962) and Wille (1964), *Fv. mexicanus* produces a loud buzzing and vibrates pollen out of the anthers. This technique is also used by some euglossine and anthophorine bees, but not by honeybees.

An incomplete review given in this section suggests that flower preference of each bumblebee species is expressed as an interaction of species specificity and

environmental conditions. The nature of this interaction is complicated. The species specificity exhibits sometimes a fixed innate tendency, probably being stronger in some species, e.g. those of *Megabombus*, but apparently not so rigid as in genuine oligolectic species. Perhaps it gives a broad framework of variable sizes, within which each species adjusts its flower visits by learning various environmental conditions.

21. Size difference among females

Bumblebee exhibit a conspicuous size polymorphism not only between queens and workers but also among workers. This relates to the problem of caste determination, which was recently experimentally analysed by Röseler (1967, '70) and Röseler and Röseler (1974), using *Bo. terrestris* and *Pr. hypnorum*. Röseler also published two reviews on the same problem (1974, '75).

Size variation among workers has been recorded in relation to season or colony age, biotope, colony size, and position of larvae within the nest as well as within a batch. As a case of specific differences, Plowright and Jay (1968) showed that worker size generally increased during colony development in *Pr. perplexus* but not in *Bo. terricola* and *Pr. ternarius*.

Since Sladen (1912), it has generally been accepted that size variation is more continuous in pocket makers than in non-pocket makers. Some previous records are cited:

Size variation larger in carder bees than underground nesters (Sladen 1912); Worker-queen difference larger in *Bo. affinis* and *terricola* (Plath 1934); Worker-queen difference arranged, *Bo. lucorum, terrestris, Ml. lapidarius* > *Pr. pratorum* > *Mg. hortorum* > *Th. humilis, pascuorum, sylvarum* (Cumber 1949); Queens and large workers rather continuous in *Bb. nevadensis, Fv. fervidus* and *californicus* (also in *Fv. pennsylvanicus*, Frison 1930), but discontinuous with lesser worker variation in *Sb. appositus* and *borealis* (Hobbs 1965a, 1966a, b); Workers and queens continuous in *Pr. hypnorum*, discontinuous in *Bo. terrestris* (Röseler 1967); Workers and queens continuous in *Bb. nevadensis, Cl. rufocinctus, Fv. fervidus, Pr. perplexus*, discontinuous in *Bo. occidentalis, Pr. ternarius* (Plowright and Jay 1968); Workers and queens continuous in *Mg. consobrinus, hortorum* and *Thoracobombus* spp., especially *Th. pascuorum*, discontinuous in *Alpinobombus, Ag. wurfleini, Bombus, Pyrobombus, Sb. distinguendus* and *subterraneus* (Løken 1973).

Løken (1973) noted the queen-worker discontinuity of *Pyrobombus* including *Pr. hypnorum*, which showed a continuity according to Röseler (1967). The actual relation is perhaps *Bombus* > *Pyrobombus* > *Thoracobombus*. In general the enumerated cases favor the assertion of the more conspicuous queen-worker continuum in pocket makers. Mainly based upon observations with *Th. pascuorum*, Cumber (1949) explained this as follows: The larvae separate themselves by spinning flimsy silken partitions and fix their positions within the batch at fourth instar. In pocket makers, such spatial fixation and the fixed position of the feeding pocket results in some larvae which are remote from the pocket and receive less food and became smaller. However, this explanation is insufficient to explain the size polymorphism

(cf. also Röseler 1975): 1) In *Ev. atratus*, a pocket maker, the difference appears before spinning partitions (Sakagami, Akahira and Zucchi 1967). 2) If the final instar larvae are fed by direct regurgitation in all subgenera (Hobbs 1964a~1967, cf. 12. 7.), differential nutrition needs not be more marked in pocket makers. 3) If queen larvae of some pocket makers receive additional food through the permanent orifice (12. 7), the feeding pocket would not be responsible for the size difference between queens and workers. 4) Queen-worker continua were found in the colonies of *Fv. fervidus* and *Sb. borealis*, which were forced to rear all larvae by regurgitation (Plowright and Jay 1968).

The differences exist not only between pocket and non-pocket makers but within each of these two groups. Within pocket makers some *Thoracobombi* seem particularly gradual as to size variation. In non-pocket makers, *Bombus* s. str. seems outstanding for the clear segregation of queens and workers compared to *Pyrobombus*. This corresponds well to the recent discovery by Röseler (op. cit.), who confirmed that queens and workers are continuous in size but separable by a specific protein in *Pr. hypnorum*, while discontinuous in size in *B. terrestris*. In *Pr. hypnorum* the caste determination occurs in the fourth instar, a time of excess feeding to the prospective queen larvae. In *Bo. terrestris* the determination takes place during the first three larval days. Older larvae of prospective workers cannot develop into queens either through maximal feeding nor by application of juvenile hormone during the fourth instar.

Specific differences are expected within a subgenus, as suggested by the difference between *Pr. perplexus* and *ternarius* cited above. Among five Neotropical lowland species of *Fervidobombus*, *Fv. morio* differs from others by a marked queen-workers continuum (Moure and Sakagami 1962). These items of evidence suggest the need for closer comparative studies of various species without stressing the difference between pocket makers and non-pocket makers.

Concerning the relation between size and worker performance, it is asserted that larger workers tend to participate in foraging more than smaller ones (*Th. pascuorum*, Richards 1946, Brian 1952; *Bo. lucorum*, *Th. pascuorum*, Cumber 1949; *Mg. hortorum*, Röseler 1974). The tendency seems only quantitative except that dwarf workers seemingly seldom leave the nest (Sakagami and Zucchi 1965, Röseler 1974).

22. Production of sexual broods

It is well known that not all bumblebee colonies rear sexual broods at the climax. For instance, among 80 colonies of *Th. pascuorum* examined by Cumber (1953, ref. Free and Butler 1959), 48 did not produce sexuals, 9 produced only males, 10 produced less than eight queens each and only 13 produced more than one queen. In general only colonies attaining sufficient size seem to produce sexual. But Sladen (1912) reported failure to produce sexuals in a strong colony of *Pr. pratorum*. The importance of an increased worker/larva ratio for the production of sexuals was stressed by Cumber (1949). Under the influence of this

factor, some specific differences are expected in view of the specific differences in colony size, appearance of sexuals (cf. 26), and mechanism of caste determination (cf. 21, 23). K.W. Richards (1975) also reported the variability of the ratio of colonies which produced sexuals in some Alberta species accepted artificial nests (percentage of domiciles produced sexuals): *Pr. frigidus* 32.6, *Pr. ternarius* 40.0, *Pr. bifarius* and *flavifrons* 42.8, *Fv. californicus*, 51.8, *Bo. occidentalis* 63.1, *Cl. rufocinctus* 67.4, *Sb. appositus* 80.0, *Pr. mixtus* 87.5.

At the change from worker to sexual production, mixed broods appear in some species, e.g. *Th. pascuorum*, *Mg. hortorum* (Cumber 1949), *Bo. terricola*, *Pr. ternarius* (Plowright and Jay 1968), *Bo. ignitus* (Katayama 1973). Probably this is widespread to many species, but precise interspecific comparisons are scarce except for the records by Plowright and Jay.

23. Laying workers

In bumblebee colonies queens inhibit the development of worker ovaries, though not so perfectly as in honeybees. Ovarially developed workers in queen-right colonies are not so rare as in honeybees, especially near the climax of colony development (*Bo. lucorum*, *terrestris*, less frequently in *Mg. hortorum*, *Th. pascuorum* Cumber 1949). Early death of the queen increases the number of such workers. K.W. Richards (1975) found the oocyte over 1.0 mm long in 9.4% of 617 examined workers of some Alberta species. Laying behavior by workers is often irregular, not exhibiting the regular sequence achieved by queens (cf. 19), though the linkage between laying and sealing is maintained (*Bo. ignitus*, Katayama 1967). From the results obtained in *Bo. terrestris* and *Pr. hypnorum* and from observations by Free (1957), who confirmed ovary development of workers of *Pr. pratorum* and *Th. pascuorum* captured in the field, Röseler (1968) concluded that the worker ovaries were able to develop within ten days after emergence. In isolated workers of *Bo. terrestris* and *Pr. hypnorum*, workers can oviposit five days after emergence (Röseler 1974). But the ovaries seem to develop more frequently in house bees than foragers (O.W. Richards, 1946, *Th. pascuorum*). This corresponds to what is known in honeybees (e.g. Sakagami 1959) and stingless bees (e.g. Akahira, Sakagami and Zucchi 1970), though age-linked polyergism is less pronounced in bumblebees. On the other hand, dwarf workers which seldom leave the nests hardly develop their ovaries (*Fv. atratus*, Zucchi 1973). Some specific differences in the appearance of laying workers has been recorded. According to Cumber (1949) small and medium sized workers tend to develop ovaries more frequently than larger ones because they survive longer by staying more in nests (this contradicts the statement by O.W. Richards, op. cit.), but in *Ml. lapidarius* larger workers are more apt to develop ovaries. On the other hand, K.W. Richards (1975) found no correlation between size and ovarian development in Alberta species. Cumber also wrote that laying workers appeared more frequently in non-pocket makers than in pocket makers, e.g. *Bo. terrestris* and *lucorum* than *Th. pascuorum* and *Mg. hortorum*, in the presence of the queen. This is noteworthy because it is opposite

to the degree of caste differentiation (cf. 21).

The contribution of laying workers to male production may be variable among species. Although in part depending on the particular life cycle in tropical climates (cf. 27), 80% of the males are produced by workers in *Fv. atratus*. Moreover, inseminated workers are rather frequent in this species, playing an important role in the perpetuation of its perennial colonies by functioning as vicarious queens at the earlier death of the old queen (Zucchi 1973). The percentage of males produced by workers in temperate species is unknown but may be much lower (cf. K.W. Richards 1975). In *Bb. nevadensis*, Hobbs (1965a) observed a nest which was established by some orphan workers. Some pots were made and males were produced. One worker remained in the nest and acted as the vicarious queen.

24. Behavior of newborn sexuals

The mating behavior of males varies among species, and can be divided into the following types (Free and Butler 1959, Haas 1967, Schremmer 1972):

I. Males hover at nest entrance and mate with queens which are leaving nests: *Sb. subterraneus*, *Th. ruderarius* (Free and Butler 1959); *Fv. fervidus*, *Sb. appositus* (Hobbs 1966a, b).

II. Males establish definite flight courses and stop at particular points along the course to mark these with scents produced from mandibular glands. The courses of different males often overlap and the marking points are frequently in common (Frank 1941, Haas 1947, '60, '67, cf. below).

III. Type intermediate between I and II, i.e. the mating course involves a nest of the same species as the visiting place: *Rd. pomorum*, *Th. humilis*, *ruderarius* (Haas 1967).

IV. Formation of a territory where the owner male awaits the arrival of queens. Plath (1930, '34) erected a biological group *Aicarrenia* for *Bb. auricomus*, *Sp. griseocollis* and *morrisoni*, the males of which possess territories and large eyes. Closer observations were made with *Md. mendax* (Haas 1960) and *Cf. confusus* (Schremmer 1972). According to Schremmer, *Md. mendax* retain scenting behavior but *Cf. confusus* responds purely optically. Hobbs (1965a) recorded similar behavior for *Bb. nevadensis* in cage. Males of *Rb. robustus* seem to behave similarly (Pijl and Dodson 1966, ref. Schremmer 1972). As these subgenera included in *Boopobombus* are likely to represent several different phyletic lines, their territorial behavior may be an outcome of parallel evolution.

Detailed observations have been made on the type II. The levels of the flight courses differ among species: *Ml. lapidarius* (tree top) > *Mg. gerstaeckeri*, *Th. sylvarum* (bushes and shrubs) > *Bo. terrestris* (herbage) > *Mg. hortorum*, *Pr. patroum*, *Th. humilis* (ground). But according to Haas (1967) such specificities vary seasonally. When new queens are available, the male flight course of *Bo. lucorum* is the highest, covering branches of big trees up to 30 m, but after the disappearance of queens males fly above the herbage. In *Bo. terrestris*, too, three

flight courses are distinguished, herbage, shrubs and bushes, and tree top. Once a male chooses one of them, he tends to repeat it. Further, in high mountains, the area covered by flight courses becomes larger, the height of scenting sites becomes variable, and daily regular cruising is preceded by non-directional scout flights. In the mountainous populations of *Th. humilis*, flight courses are at bush and shrub level and, in contrast to the lowland populations, males are not attracted by nests, even if the course passes by them.

These records suggest the necessity for closer studies of various species classified into four types shown above. The type IV may be distinctive, but the relations among other three types must be studied in connection with environmental and life history differences. Specific differences in scenting behavior was described by Awram (ref. Alford 1975): *Pr. pratorum* marks with scent 3~5 times at any one site, *Bo. lucorum*, *terrestris* and *Mg. hortorum* do 2~4 times, *Th. pascuorum* 1~3 and *Ml. lapidarius* only once. *Ml. lapidarius* usually marks several sites in succession, but other species usually do not so.

Intranidal mating has been observed in some species. Recent references are *Fv. pennsylvanicus* (Frison 1930), *Cl. rufocinctus*, *Fv. fervidus* and *Sb. borealis* (Hobbs 1965b~1966), *Pr. ardens* (Katayama 1964). In *Fv. pennsylvanicus* and *Cl. rufocinctus*, intersib mating is recorded. But, according to K.W. Richards (pers. com.) intranidal mating in *Cl. rufocinctus* is exceptional even if occurs. Hobbs (1965a, 1967) observed no intranidal mating in *Bombias* and *Pyrobombus* species observed by him. From the observations of mating pairs of *Pr. bifarius* and *huntii* flying back to and entering nests, Hobbs (1967) interpreted an intranidal pair of *Pr. pratorum* recorded by Free and Butler (1959) as a similar case, but Katayama noted ten cases of intranidal mating in *Pr. ardens*, some of which were definitely intersib. How frequently such intersib mating occurs is interesting in connection with the degree of population viscosity (Hamilton 1972).

Many species can mate in captivity (Free and Butler 1959, Pouvreau 1963) and the occurrence of intranidal mating may partly depend on the easiness of releasing copulatory act under confinement. According to Plowright and Jay (1966), *Cl. rufocinctus* mated in small containers unlike *Bo. terricola* and *Pr. ternarius*. *Fv. atratus* is also ready to copulate within narrow boxes (Garofalo, unpub.).

New queens make their departures several days after emergence, about five days in *Bo. terrestris* and *Pr. hypnorum* (Röseler 1975), 2~8 days in *Bo. lucorum* (Free and Butler 1959), 3~4 days in *Bo. ignitus* and one week in *Pr. ardens* (Katayama 1967). Katayama noted queen emergence in *Bo. ignitus* all within five days, contrasting with *Pr. ardens*, the queen emergence of which lasted one month.

Pouvreau (1963) observed multiple mating by both sexes of *Pr. hypnorum* in captivity. Hobbs (1967) also confirmed that caged queens of *Pr. huntii* mated 2~3 times but those of *Pr. bifarius* tried to enter hibernation after the first mating. With *Bo. terrestris* and *Pr. hypnorum* Röseler (1967, ref. 1973) confirmed multiple mating of queens in captivity, usually 3~4 times, for some queens up to nine times. But from the number of sperms in the spermathecae of autumn and spring queens,

he concluded that queens mated as a rule only once (*Bo. lucorum*, *terrestris*, *Mg. hortorum*, *Ml. lapidarius*, *Pr. pratorum*, *Th. humilis*, *pascuorum*, *sylvarum*) except for *Pr. hypnorum*, which seemed to mate 2~3 times (Röseler 1973). The sperm counts in both queens and males of *Fv. artatus* and *morio* (Garofalo 1973) also indicated single mating.

Many queens do not return to their nests after departure, but some return and participate in various duties including foraging, wax production and even nest defense (*Bo. terrestris*, Free and Butler 1959, Haeseler 1974; *Bo. affinis*, Plath 1934; *Al. polaris*, K.W. Richards 1973). Such behavior may appear only under particular conditions, e.g. shortage of workers (Free and Butler 1959), early queen production (Haeseler 1974). According to Röseler (1974), queens are ready to mate for 2~3 weeks after emergence. Confining them 3~4 weeks causes loss of this readiness, leading to production of wax and eggs and rearing of larvae. A colony of *Pr. hypnorum* provided with excess food and artificial heating produced many queens and a few workers. These queens participated in building, foraging and brood rearing but the workers did nothing (Lehmensick and Stein 1958). Horber (1961, ref. Plowright and Jay 1966) maintained a laboratory culture of *Pr. hypnorum* for five generations and asserted that diapause was not obligatory for this species (cf. also Röseler 1975). This finding is noteworthy because it relates to the colony cycle discussed in 27.

25. Hibernation

In bumblebees only newly emerged queens enter the hibernation. Many miscellaneous records have been published on this problem. Here are cited only two recent careful studies, Hobbs (1965a~'68) on the species of Alberta and Alford (1969, '75) on the British species.

Unlike nest foundation, the hibernating queens always dig in the soil by themselves. Hobbs observed behavior of queens put in the flats filled with soil or soil-sphagnum mixture, or in the hibernation cages the bottoms of which were made by a mosaic of sward and bare soil patches. Depths (in inches) of hibernacula were recorded:

Al. balteatus 1.7 (range 1.5-3.0, 14 queens), *Bb. nevadensis* 4.5 (3~7, 10 queens) in the loose soil in flats and 3 (1~6, 23 qq.) in compact soil in cages, *Bo. occidentalis* 2 (1 q), *Cl. rufocinctus* 1.7 (1~2.5, 11 qq) in flats and 1.1 (1~1.5, 14 qq) in bare patches of swards, *Fv. californicus* (1, 1, 2 in 3 qq) in cages, *Pr. flavifrons* 4.0 (2 qq) in loose soil and 1.5 (1 q) in compact soil, *Pr. frigidus* 1.0 (1 q) in flat, 1.2 (2 qq) in swards, *Pr. huntii* 3.0 (1.5~5.0, 16 qq) in flats, 2.1 (0.5~4.5, 36 pp) in swards, *Pr. nearcticus* 4.1 (0.7~7.5, 53 qq) in sandy soil, *Pr. sylvicola* 1.0 (8 qq)~1.5 (2 qq) in cages.

Hobbs (1965a) found no difference of super-cooling points between a prairie species, *Bb. nevadensis*, and a woodland species, *Cl. rufocinctus* (-19°C stored at 0.5°C, -14°C stored at 5°C) and assumed that *Cl. rufocinctus* could not hibernate in prairie because it does not dig deeper. Later he abandoned this hypothesis

because no difference in hibernation was found between *Pr. huntii*, a prairie species, and some other not typically prairie species (1967).

From the choice of various slopes of the soil in the cage, mainly by *Pr. huntii* and *nearcticus*, he concluded that steep north or west slopes were preferred for hibernation (1967). Perhaps caused by spatial limitation, up to four queens of *Bb. nevadensis* were found in common hibernacula, which were larger than those serving only one.

Alford (1969, '75) made an extensive field survey. The preference for hibernacula was variable among species. *Mg. hortorum* and *Ml. lapidarius* (both late emerging species) prefer banks. The preference for directions of slopes was $NW \gg N \approx W > NE \gg SE \geq S = SE > S$, being similar to the results by Hobbs (op. cit.). On the other hand, *Bo. lucorum*, *terrestris* and *Pr. pratorum* (all earlier species) prefer soil near the bases of the trees. But *Bo. lucorum* is quite adaptable for sites. Two queens were found in the folds of a curtain in a north-facing room. In some species, especially *Pr. hypnorum*, queens sometimes hibernate in stone walls and rotten tree stumps. Strangely it is difficult to find the hibernating queens of *Thoracobombus*. Only three queens of *Th. pascuorum* were found under herbage.

The depth of hibernacula differs between later species (*Ml. lapidarius*, *Mg. hortorum*) and earlier species (*Bo. lucorum*, *terrestris*, *Pr. pratorum*, *Th. pascuorum*). The former groups prepares hibernacula well below the boundary between litter and soil layer, whereas the latter group hibernates at interface between litter and soil.

Plath (1927, ref. 1934) recorded the hibernation in mass of *Pr. impatiens* near the maternal nest. Townsend (1951) found 86 queens of the same species within three sq. feet (2~4 inches deep), but whether the nest was near the site or not was uncertain. No such instance was found in the British species. Only three queens of *Ml. lapidarius* were found within 2 m from nests (Alford 1959).

26. Phenology and colony size

As referred to 25, specific differences in emergence of post-hibernating queens are recorded from some areas (cf. Sladen 1912, Plath 1934, Free and Butler 1959). For the British species Alford (1975) distinguished as follows: 1) Earlier species. *Bo. lucorum* (very early), *magnus*, *terrestris*, *Pr. jonellus*, *pratorum*, *Th. pascuorum*, *runderarius*; 2) Later species. *Cl. cullumanus*, *Kl. soroensis*, *Mg. hortorum*, *runderatus* (later than *hortorum*), *Ml. lapidarius*, *Sb. subterraneus*, *Th. humilis*, *muscorum*, *sylvarum*. Pouvreau (1972) proved a higher heat production by the queens of *Bo. terrestris*, an earlier species, than by those of later emerging *Ml. lapidarius*. Combining phenology and ovarian development, Medler (1962) divided the Wisconsin species in four groups: 1) Very early. *Bo. terricola*, *Pr. bimaculatus*; 2) Early. *Bo. affinis*, *Pr. ternarius*, *Sp. griseocollis*; 3) Mid season. *Bb. auricomus*, *Fv. fervidus*, *Pr. impatiens*, *Sb. borealis*; 4) Late. *Cl. rufocinctus*, *Fv. pennsylvanicus*. Hobbs (1965a~1968) and K.W. Richards (1975) made detailed studies with the species in Alberta. Richards recognized the following order of emergence. *Pr. frigidus* = *Pr. bifarius* > *Pr. mixtus* = *Bo. occidentalis* = *Pr. flavifrons*

>*Pr. ternarius*>*Cl. rufocinctus*>*Fv. californicus*>*Sb. appositus*. The difference in peak dates was 5~7 weeks between *Pr. frigidus* and *Sb. appositus*.

Contrary to previous studies, K.W. Richards observed the development of oocytes, to some degree, in new queens before hibernation. He assumed two different strategies between early and late emerging species. The former group, e.g. *Pr. bifarius*, do not develop oocytes in autumn, but the queens emerge earlier in spring and the ovaries enlarge slowly. In the latter group, e.g. *Sb. appositus*, the oocytes appear in autumn and ovarian development after hibernation is rapid.

The annual cycle of the temperate species can be divided into several phases as given in the introduction. The time of beginning and duration of each phase vary according to environmental conditions, but some species-specificities exist. The most conspicuous case is the short annual cycle in some species of *Pyrobombus*. *Pr. pratorum* is famous for earlier appearance of sexuals, even in late May, and the short colony cycle with the dissolution in July (Free and Butler 1959). *Pr. ardens* is its eastern counterpart, sexuals appearing in June and all colonies dying in July (Miyamoto 1957b). Although less conspicuous, the colonies of *Pr. hypnorum* are also short lived (Postner 1952, Haeseler 1974), whereas some other *Pyrobombus* species seem more long lived, e.g. the species observed by Hobbs (1967) and Richards (1975) in Alberta. Among the British species the colonies of *Th. pascuorum* are the most long lived, lasting from late April or early May to September or later. *Th. sylvarum* also makes lasting colonies but founded later. The colonies of *Bo. lucorum* and *terrestris* become very large but end in mid to late August. (Alford 1975).

A further elaboration of the deviation from the annual cycle is the occurrence of two generations per year. Meidell (1968) showed *Pr. jonellus* as having two generations in Norway. The same sequence is taken occasionally by *Pr. pratorum* (Alford 1975, England), *Pr. bifarius*, *frigidus* (Hobbs 1967, Alberta) and possibly by *Pr. lapponicus* (Løken, Scandinavia). As an unusual case, Plath (1934) recorded an orphan colony of *Bo. affinis* succeeded by a young queen, which produced more than 100 workers in September and many queens in October. As cited in 24, Horber (1961) asserted that the diapause was not obligatory in *Pr. hypnorum*. These records suggest comparison of the annual life cycle of temperate species with the perennial cycle of some tropical species referred to 27.

Partly but not necessarily linked with colony life span is the colony size attained at the climax. Many records have been published for various species. Here are mentioned only some examples.

For the Nearctic species Plath (1934) gave the following figures (total individual number): *Bo. affinis* 180, *Bo. terrestris* 50~150, *Fv. fervidus* 50~125, *Pr. bimaculatus* >60, *Pr. impatiens* >450, *Pr. ternarius*>100, *Pr. vagans* >70. For the species in Alberta, Hobbs (1965a~1968) gave the number of cocoons per nest as follows: *Bb. nevadensis* 55, 86 and 139 in three queen producing colonies; *Cl. rufocinctus* 65~160, maximum 430; *Fv. californicus* 30~80; *Fv. fervidus* 200~300; *Pr. huntii* maxima 523 and 772; *Sb. appositus* 70~170. Some records for the European species: *Bo. lucorum*, *terrestris* 200

~300, other underground nesters, e.g. *Mg. hortorum* 100, carder bees 50 (Sladen 1912, total individual number); *Bo. lucorum*, *terrestris* and *Ml. lapidarius* 300~400 workers being more populous than other species (Free and Butler 1959); *Bo. terrestris* and *Ml. lapidarius* 300~400 workers, other species 50~100 (Röseler 1975). The largest colonies so far known are *Fv. medius* in Mexico (2,183 offspring, Michener and La Berge 1954) and *Fv. transversalis* in the Equatorial Brazil (3,056, Dias 1958).

Interestingly the number of sperms carried by each post-hibernating queen is roughly comparable to the colony size attained; nevertheless this is not a factor limiting the colony growth (Röseler 1973): *Th. humilis* (12,200), *Pr. pratorum* (13,200), *Mg. hortorum* (14,700), *Th. pascuorum* (17,300), *Th. sylvarum* (19,900), *Pr. hypnorum* (23,300), *Bo. lucorum* (33,500), *Ml. lapidarius* (41,600), *Bo. terrestris* (52,800). Garofalo (1974) gave the values for two Brazilian species, the colonies of which become very large: *Fv. morio* (49,200), *Fv. atratus* (68,990).

27. Colony cycle and social organization

As mentioned in the introduction, the life cycle of temperate species consists of the several phases schematized in Fig. 1. There occur two deviations from the cycle mentioned. One is the succession of two generations, which is expressed by the duplication of phases IV~X and I~II in Fig. 1. This is possible only in the species with short colony life (cf. 25). Another is the usurpation of a colony by another queen of the same or different species, as discussed in 28.

Bumblebees are unique among social insects in the extension of their distributional range to the high Arctic (Skorikov 1937, Panfilov et al. 1960, K.W. Richards 1973). It has been suggested that under the severe Arctic climate, worker production may be omitted, the life cycle reverting to that of solitary bees (e.g. Sparre-Schneider 1906). However, O.W. Richards (1931) showed the presence of workers in most species of *Alpinobombus*, though numerically far inferior to those in other subgenera. Hasserlot (1960) obtained one batch of workers in a nest of *Al. balteatus*. Løken (1961a, 1973) obtained some worker batches in the nests of *Al. alpinus*, *arcticus* and *balteatus* in Scandinavia. K.W. Richards (1973) definitely confirmed worker production by *Al. polaris* at Lake Hazen, Ellesmere Is. (81°49'N). Further, *Al. hyperboreus*, which has been cited as supporting the presence of solitary life cycles by the scarcity of workers, was proved to be parasitic on *Al. polaris* (Milliron and Olivier 1966, K.W. Richards 1973), though some workers are known in Northern Europe (Løken 1973). It is unknown whether some colonies of *Alpinobombus* except *Al. hyperboreus* can produce sexuals not preceded by worker production. At the social level attained by bumblebees, the complete reversal to solitary life seems unlikely, which is known in some eusocial halictine bees, e.g. *Lasioglossum calceatum* (Scopoli) (Sakagami and Munakata 1972).

In warm temperate and subtropical lowlands, bumblebees diminish both in species and individuals. In Corsica, *Bo. terrestris* disappear in dry, late summer. Queens appear after the autumn rains, workers appear in December, and males in January, though at least some colony activities continue through the spring

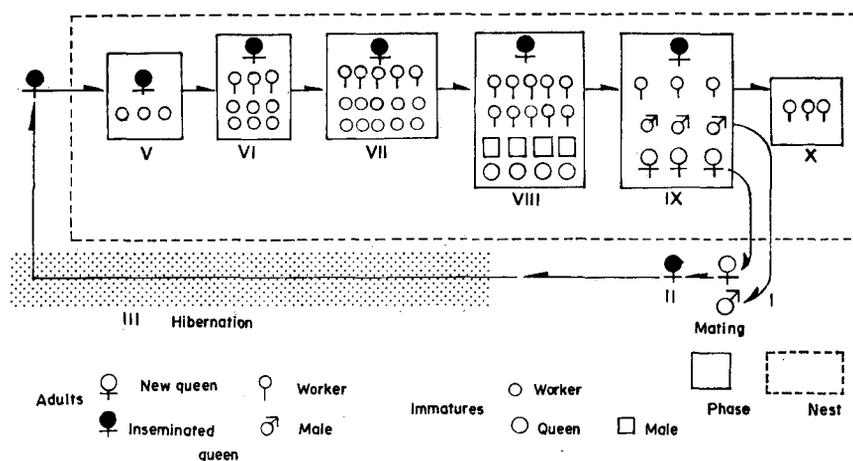


Fig. 1. Schematized life cycle of temperate bumblebees. For simplicity mating is shown as if between sibs. (Phase IV dropped at lefthand).

(Ferton 1901). Year round flight activity has been reported in the species introduced from England to New Zealand (Cumber 1954, Gurr 1961). But only in South America do bumblebees flourish in a genuine tropical climate.¹⁾ The life cycle of these Neotropical lowland species different from that of their temperate congeners was once suggested by v. Ihering (1903), who assumed that colonies are perennial, polygynic and founded by swarming. These assumptions have been cited without further comments until recent studies made in Brazil.

Certainly not all colonies are perennial throughout tropical or subtropical lowlands of South America. Judging from the phenology in Southern Brazil (Sakagami and Laroca 1971), most, if not all, colonies of *Fv. bellicosus* are annual there. Michener (1974) dug a queen of this species from the soil in winter in the same area. Even most colonies of *Fv. transversalis* in the Amazonic forests seem to succumb within the year (Dias 1968). However, the persistence of a colony of *Fv. atratus* more than one year was first confirmed in the State of São Paulo by Kerr (cf. Moure and Sakagami 1962). A colony of this species reared in an observation hive survived from autumn to winter, producing workers, not sexuals (Sakagami and Zucchi, 1965, Sakagami, Akahira and Zucchi 1967). Later the life cycle of this species was precisely followed with colonies reared in observation hives by continuous records taken for ten years (Zucchi 1973).

The results are summarized below, based on Fig. 2, which corresponds to Fig.

1) Discovery of a queen from the Equatorial Africa (Tkalcù 1966) requires further critical study. The species, *Fv. abdictus*, was described as closely similar to *Fv. brevivillus* of North Eastern Brazil (cf. Moure and Sakagami 1962). After comparing the original description with a long series of the queens of *Fv. brevivillus*, I failed to find any characters which were out of the variation range of *Fv. brevivillus*.

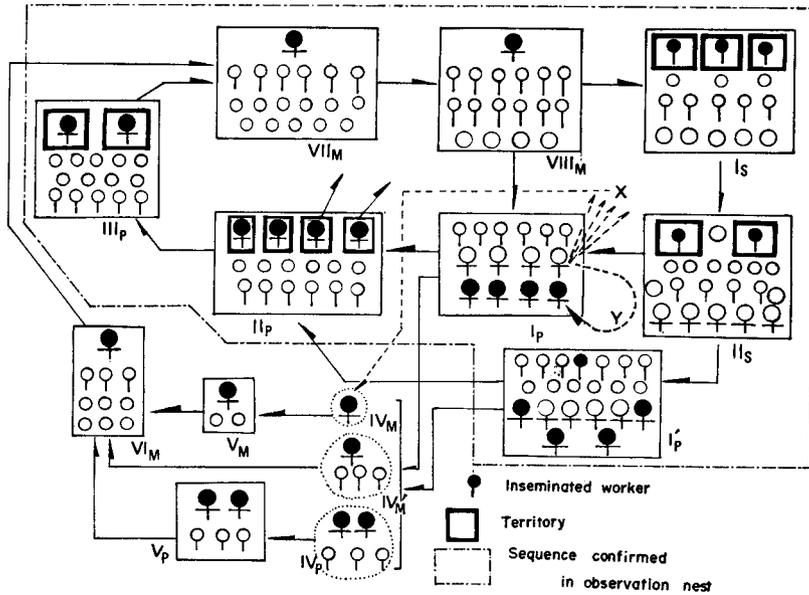


Fig. 2. Schematized life cycle of *Fv. atratus*. Symbols not explained are the same as those in Fig. 2. For simplicity males are omitted.

1 except for the omission of male production. The explanation starts from phase VII_M, phase of active worker production. This phase goes to VIII_M, queen production. The colonies do not succumb as in temperate species. Many new queens leave the nest (Fig. 2, I_P, X), but some, after mating, return to the original nest or to alien ones (I_P, Y). Each of these queens occupies a definite area within the nest, produces egg cells and violently defends the area against other queens. In contrast to the relation among workers in queenless colonies (Free 1955a), this territorial defense (Figs. 3, 4) never leads to social dominance. Consequently many queens are killed or leave the nest and the number of territory owners gradually decreases (III_P, cf. Fig. 4), until finally the colony reaches the monogynic phase (VII_M).

As workers are completely indifferent to these territorial combats and are allowed to enter any territory and to rear the brood there indiscriminably, contributions by defeated queens are absorbed into the monogynic phase. Thus, the colony alternates between two phases, monogynic (VI~VIII) and polygynic (I~III). But there often appears another subsidiary route. When the monogynic queen dies earlier, or, as is more usual, killed by workers at her senescence, some large workers mate and form territories (I_S~II_S) within the nest until the appearance of new queens (I'_P). As this substitute phase (S) is optional, the colony cycle is formulated as *n*PM(S). The phase S would seldom occur in the species with marked queen-worker difference (cf. 21), even if such species would survive in

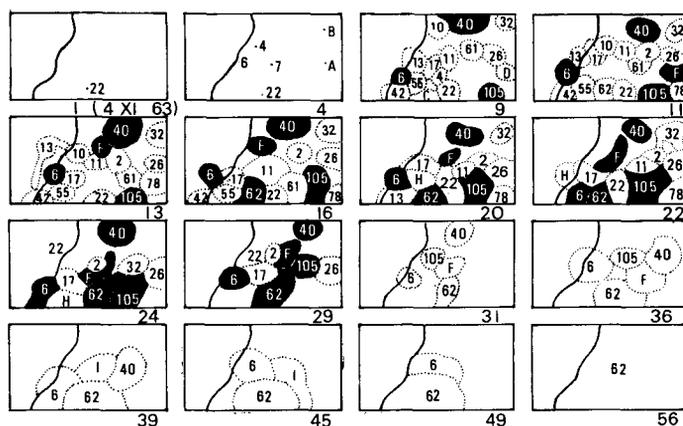


Fig. 3. Polygynic phase with territorial rivalry in *Fv. atratus*, from a 56 day record by Dr. R. Zucchi, starting from Nov. 4, 1963, until monopoly was attained by Queen Nr. 62 (Redrawn from Zucchi 1973, by his permission). Numerals and letters indicate individually marked queens and the contours, the extent of territories. Several persistent territories are shown as black areas. The oblique line at the left is the boundary of combs within the observation hive.



Fig. 4. Territories of three queens of *Fv. atratus*. Queens shown with arrows and territories with broken lines. Other individuals are workers. Photo by Sakagami at a colony reared by Dr. R. Zucchi.

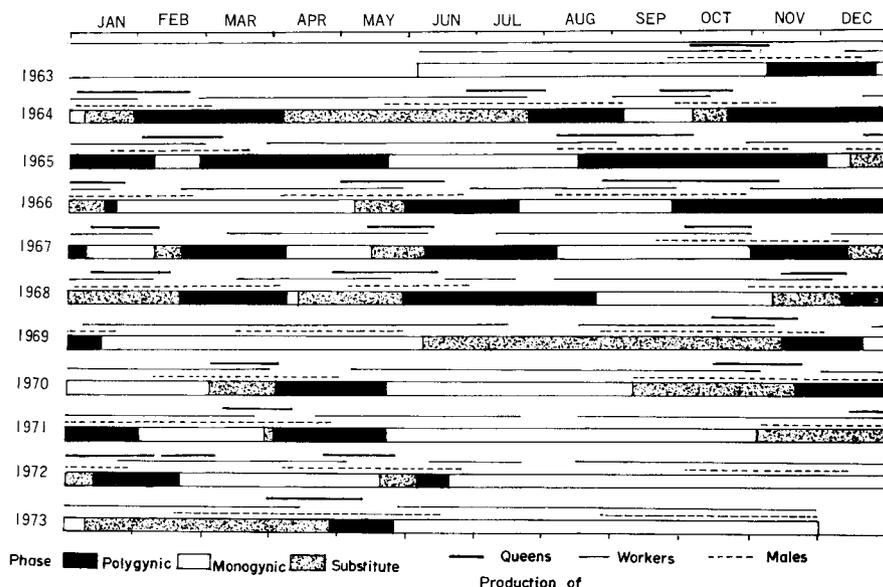


Fig. 5. Ten years continuous observation of a colony of *Fv. atratus*, showing alternation of mono- and polygynic phases (Redrawn from Zucchi 1973, by his permission).

tropical climates. Fig. 5 shows the alternation of these phases in a colony observed by Dr. R. Zucchi for ten years. That alternation of mono- and polygynic phases appears in natural conditions is proved by certain nests containing alternate layers of queen and worker cocoons. Interestingly, a similar territorial combat among females is known in *Bo. terrestris* introduced in New Zealand (Cumber 1963, ref. Michener 1974). Cumber writes that "antagonism gathers greater momentum, and precludes the possibility of the development of perennial nests." It must be stressed that in *Fv. atratus* the perennial nests are maintained despite of periodical antagonism.

How then is nest foundation? Is a nest started by a solitary queen as in temperate species, or by swarming as suggested by v. Ihering? The occurrence of solitary foundation is evidenced by the discovery of an incipient nest for *Fv. morio* (Milliron 1961a) and for *Fv. atratus* (Sakagami, Laroca and Moure 1967). Probably queens who do not return to the nest (Fig. 2, I_P, X) found the solitary nest, producing a monogynic colony through the route IV_M-V_M-VI_M-VII_M (Fig. 2). On the other hand, the colony foundation by swarming was recently observed in *Fv. atratus* (Garofalo 1974), who studied the foundation of a polygynic association issued from one colony, with some worker joiners from other colonies. In this case, the route to the monogynic colony is IV_P-V_P-VI_M-VII_M (Fig. 2), but the monogynic swarming (IV_M-VI_M-VII_M) is also theoretically not excluded. Two

such polygynic swarmings were observed. And Sakagami, Zucchi and Garofalo (unpub.) got a colony of *Fv. atratus* containing more bees than cocoons, apparently produced by swarming. Thus, three assumptions by v. Ihering were confirmed 70 years after publication, though with some limitations. Comparatively, *Fv. morio* which has the poorest queen-worker differentiation, the *queens* from the same batch behave differently, one functioning as the egg layer, while others as workers and even foragers, without severe territorial combat (Garofalo unpub.).

Bumblebees also live in the tropical mountains. Many of these species form small, endemic subgenera (*Rufipedibombus* in S.E. Asia, *Robusto-*, *Funebri-*, *Rubicundi-*, and *Coccineobombus* in the Andes). The life cycles of such species should be similar to those of lowland tropical species. The climate is very uniform throughout the year, even if not very hot. Recently Michener and Amir (in press) described the phenology of *Rf. rufipes*. Queens, males and workers are active throughout the year. Probably queens and workers are produced in every month. New colonies are evidently established by lone queens as in other species. But three worn queens were seen leaving a single nest, suggesting the occasional remaining together of the queens, leading to perennial colonies like those of *Fv. atratus*.

28. Usurpation

Apart from the specialized parasitic bumblebees, *Psithyrus*, usurpation is frequent in bumblebees, both con- and interspecifically. As to conspecific usurpation Sladen (1912) found a nest containing more than 20 corpses of queens and mentioned a strong tendency to usurpation in *Bo. terrestris* and *Ml. lapidarius*. The tendency is also known in other species, e.g. *Pr. pratorum*, *Sb. subterraneus*. He recorded a case in *Th. ruderarius* but commented on the rarity of usurpation in carder bees. However, Voveikov (1953) recorded beside *Bo. lucorum*, *Kl. soroensis*, *Ml. lapidarius*, *Sb. subterraneus*, usurpation in *Th. humilis*, *pascuorum*, *ruderarius*, *sylvarum* and *veteranus*. As for the Nearctic species, Frison (Plath 1934) recorded the cases in *Bo. affinis*, *Fv. pennsylvanicus* and Hobbs (1965b~1967) those in *Cl. rufocinctus*, *Pr. bifarius*, *frigidus*, *huntii*, *mixtus*, *sylvicola*, *Sb. appositus*.

Interspecific usurpation is also recorded as follows (Usurped/Usurper):

Bo. lucorum/terrestris, *Bo. lucorum* is milder and less vigilant (Sladen 1912); *Sb. subterraneus/distinguendus* (Lindhard 1912, ref. Free and Butler 1959); *Sp. griseocollis/Fv. pennsylvanicus* (Frison 1930); *Bo. terricola/affinis* (Plath 1934); *Sb. subterraneus/distinguendus/subterraneus*, *Th. humilis/veteranus/humilis*, *Th. humilis/veteranus*, *Th. sylvarum/veteranus*, *Th. ruderarius/veteranus*. An extreme case, *Th. humilis/humilis/veteranus/veteranus/veteranus* (Voveikov 1953); *Sb. appositus/borealis* (Hobbs 1966b); *Pr. flavifrons/vagans*, *Pr. ternarius huntii* (Hobbs 1967); *Th. schrencki/pseudobaicalensis* (Sakagami and Nishijima 1973).

More detailed observations were made by K.W. Richards (1975). Usurpation was recognized in all common Alberta species except *Pr. flavifrons* as follows:

Invaded/Invader	fri	bif	mix	ter	occ	cal	ruf	app
<i>Pr. frigidus</i>	9	1	3		1		1	
<i>bifarius</i>		16	1	1	1			
<i>mixtus</i>		1	2					1
<i>ternarius</i>	1							
<i>Bo. occidentalis</i>		1			20		1	
<i>Fv. californicus</i>						4		
<i>Cl. rufocinctus</i>							22	
<i>Sb. appositus</i>								6

Conspecific cases occupied 83.2% and interspecific cases 16.8%. Unless making planned observations as did by Richards, interspecific usurpation must be recorded more often than real frequency, because it is more easily discovered by color difference between the two species concerned. This may be one of the reasons that only interspecific cases are recorded in some species cited above.

Some results of Richards are summarized: 1) Invaded nests occupied 11.0% (1970) and 9.2% (1971) of total nests, respectively 245 and 464. 2) In most cases only one invasion occurred, but sometimes up to four, e.g. one nest of *Bo. occidentalis* was invaded by three conspecific queens and another of the same species by three conspecific queens and one *Pr. frigidus* queen. 3) Success of original queens was 36% and of invaders 32.9% among 79 conspecific cases. For some particular species, *Pr. bifarius* success by owners 68%, by invaders 16% (among 19 cases), *Bo. occidentalis* 18 and 23% (23), *Cl. rufocinctus* 42 and 29% (24). 4) In conspecific cases, 55% of won queens were larger than the competitors, and 14% the same sized. 5) Among 27 usurped nests, 88.8% produced at least one sexual and 11.2% did not produce sexuals, whereas among all observed nests combined (245) 56.7% produced sexuals but 44.2% not.

The last mentioned result relates with that by Voveikov (1953). According to him, larger queens tend to usurp the nests founded by smaller queens and in *Th. veteranus* nest foundation by larger queens is very rare. He assumed that this "division of labor", earlier nesting by small working queens and later increase of colony size by larger ones, is efficient for colony development. It is regrettable that he did not give data supporting this interesting opinion precisely, because it postulates a selection operating above the colony level, unless the usurpers are ordinarily sisters of the nest founders.

In general the outcome of usurpation seems to be the elimination of either nest owner or invader. The coexistence of both by means of a dominance order as in polygynic associations in *Polistes* wasps (Pardi 1942, West-Eberhard 1969) or with a territoriality in nests as in *Fv. atratus* (26) is so far not recorded. Artificial joining of two or more queens has repeatedly been done in order to facilitate colony foundation (Plowright and Jay 1966). In most cases, only one queen survived combat, but precise observations on the social coaction have not been described. Röseler (1965) formed con- and interspecific polygynic colonies. Among those surviving, the con- (*Bo. lucorum*) or interspecific (*Bo. terrestris-lucorum*) dominance orders were observed but no territorial rivalry was recorded. The rarity of

polygynic association corresponds to the strict monogyny prevailing in bumblebees, but it is interesting that the coexistence of a bumblebee queen and an invaded *Psithyrus* female is sometimes recorded (Alford 1975).

Most interspecific usurpation occurred between species of the same subgenus, with an exception given by Frison (1930) and those recorded by K.W. Richards (1975, 92.9% being consubgeneric). K.W. Richards (1975) also recorded some cases of interspecific drifting by workers: *Pr. frigidus* (in nest of *Bo. occidentalis*), *Pr. bifarius* (*Pr. frigidus*, *Bo. occidentalis*, *Fv. californicus*), *Pr. mixtus* (*Pr. frigidus*), *Bo. occidentalis* (*Pr. bifarius*, *frigidus*, *Cl. rufocinctus*, *Fv. californicus*), *Fv. californicus* (*Pr. frigidus*, *bifarius*, *vagans*, *Bo. occidentalis*, *Cl. rufocinctus*), *Sb. appositus* (*Pr. frigidus*, *Cl. rufocinctus*).

According to K.W. Richards (1973) *Al. hyperboreus* is an obligatory usurper of *Al. polaris*. Bergwall (1970, ref. Løken 1973) reported its usurpation of a *Pr. jonellus* nest in Sweden and Løken recorded a nest of *Al. arcticus* in Greenland. But Løken (1973) cited captures of some workers of *Al. hyperboreus* in Northern Europe so that the queens might produce some worker batches in usurped nests. Yarrow (1970) assumes *Th. inexpectatus* as a similar case, parasitic on *Th. ruderarius*, because the workers have so far not been discovered and the corbiculae show a slight degeneration. But K.W. Richards (pers. com) suspects this argument by the reason that capture records of queens forms a bimodal curve, which does not exclude the possible occurrence of workers.

O.W. Richards (1927) explained the origin of the parasitic genus *Psithyrus* as a result of specialization developed from facultative usurpation. Between two closely allied, partially sympatric species, queens of southerly species appear later than those of northerly species, and tend to invade the nests of the latter as in case of *Bo. terrestris* invading the nests of *Bo. lucorum*, which is less aggressive (cf. also Reinig 1935, Weyrauch 1938). According to Plath (1934) the relation between *Bo. terricola* and *affinis* is a Nearctic counterpart. The former species is distributed more northerly and the queens appear earlier than those of the latter in the same area. But Grütte (1935) is suspicious of this idea. Alford (1975) notes frequent usurpation of the nests of *Sb. subterraneus* by its northerly consubgener, *Sb. distinguendus*. He comments that the hypothesis by O.W. Richards on the north-south relatives is not always valid. K.W. Richards regards usurpation as a particular interference type competition caused by the shortage of sufficient nest sites. Two nest entrance camouflaging species, *Pr. bifarius* and *Bo. occidentalis*, frequently practice usurpation. The entrance camouflage is adaptive to prevent usurpation (cf. 3). In case of interspecific usurpation, it is an efficient method to eliminate the competitors. Richards thinks about the resulting divergence of nest sites among the species. He is suspicious of the hypothesis by O.W. Richards. Certainly interspecific usurpation often occurs between the species not exhibiting a north-south slip of distributional ranges. Further accumulation of precise data are required. Anyhow, a specialized parasitism may develop based on interspecific usurpation than conspecific one, because the gene causing such parasitic behavior

may tend to destroy its own replica in relatives in a single interbreeding population (Hamilton 1972). Apart from the problem of usurpation, the occurrence of many "coupled species" (Doppelformen by Krüger 1920), i.e. closely allied, sympatric species, is conspicuous in bumblebees. Comparative studies of these species are fruitful to clarify the evolution of bumblebee habits.

Discussions

Among various instances reviewed in the preceding sections, many cases certainly do not deal with real specific differences, simply showing that only some particular species were observed as to the characters concerned. However, species or group specificities indubitably exist in many other characters. These characters may be divided into those apparently adaptive and those the adaptive values of which are yet uncertain. Some characters, or exactly, their conditions, may be adherent to particular taxa, while some others are seemingly the outcomes of independent evolution. Two or more alternate conditions of a given character may signify a diversification or a serial improvement. It is out of the scope of the present review to discuss these problems, because this review was prepared, first of all, in order to give a synoptic presentation of various specific differences so far described, which was necessary as a basis for closer analyses of the problems mentioned above. Only some previous opinions will be cited below. Before dealing with them, however, some comments are preceded on the observational controversies pointed out in the introduction.

Many previous records of the specific differences of bionomic characters may represent real species or group specificities. But many others seem to reflect observational errors or different responses within similar or overlapping ranges of specific behavioral plasticity, caused by particular colony or environmental conditions. The situation which cause observational controversies are explained as follows: Suppose that there are only two taxa, X and Y, with only four bionomic characters, A, B, C, D, each of which appears in only two alternate conditions, 1 and 2. Suppose also there are only two specialists, P and Q, who studied these taxa bionomically. The specific differences may be probable when both P and Q reported, for instance, X (A_1, B_2, C_1, D_2) and Y (A_1, B_1, C_2, D_2). In this case, X and Y are common in A and D, but different in B and C. But imagine the following results:

$$\begin{array}{ll} \text{P: } X (A_1, B_?, C_1, D_2) & Y (A_?, B_1, C_2, D_2) \\ \text{Q: } X (A_?, B_2, C_1, D_1) & Y (A_1, B_?, C_2, D_2). \end{array}$$

Here character A might take the same condition in both X and Y, and B different conditions in X and Y, but sufficient information is not available for either conclusion. The controversy in D may depend on either an error by P or Q, or on the different responses under different colony or environmental conditions. Thus, the results only show that two taxa seem different in character C alone. Increasing the number of taxa, characters with their conditions and of specialists,

we simulate the present status of our knowledge on bumblebee bionomics.

The accumulation of precise observations is essential for the advance of this field. Some bionomic characters are difficult to confirm without experimental interference, but others are easy to establish, provided care is taken for systematic and standardized recording of the results. It is possible that many observers have overlooked bionomic peculiarities because they were too familiar to them. To record accurately species names, conditions at observations and number of cases confirmed are indispensable. The last item is especially important for the rather plastic characters such as nest site preferences. Another very important caution is to record the "lack" of any particular features under given conditions.

1. Group specificities in bionomic characters

In spite of many ambiguities and controversial observations, some differences among species or higher taxa are evident.

The correspondence of the morphological group *Odontobombus* to the bionomic group "pocket makers" is one instance and favors the phyletic unity of this group, though pockets are also recorded in *Alpinobombus* and *Alpigenobombus* (cf. 12. 4.). All subgenera of *Odontobombus* are more or less long headed, consequently rather adapted to visit tubular flowers (cf. 20). But here the correspondence is not strict. Outside of *Odontobombus*, some species of *Sibiricobombus* are long headed and *Orientalibombus* possesses very long heads, indicating parallel evolution of this feature.

The subgenera of *Boopobombus* are characterized by enlarged eyes in males. Franklin (1954) explained this tendency by parallel or convergent evolution as an adaptation to high altitude environments, where the reduction in the density and absolute humidity of the air caused the shortening of antennae and, in compensation, the enlargement of eyes and ocelli. This hypothesis requires further critical examination. Laying of a single egg in each cell as in *Bombias* (cf. 10), must be carefully checked in the study of the nests of other *Boopobombus* groups. Judging from morphological comparisons, *Boopobombus* is a composite group involving some different phyletic lines, contrasting to the phyletic uniformity of *Odontobombus*. This is probably valid for *Anodontobombus*, too.

At the subgeneric level, *Bombus* s. str. may be the bionomically most compact group. Plath (1934) enumerated the following features common to the species of this subgenus: 1) Each batch not forming a compact cluster; 2) Loose wax cover of cells, partially exposing old larvae; 3) Deposition of pollen in large cylinders, usually built at the center of the nest; 4) Wax dark and brittle, as if mixed with black soil; 5) Males sluggish; 6) Appearance in early spring and long colony life; 7) Nests in subterranean cavities. Some of these features might not be common to all species. On the other hand, the following additional features seem common to many, if not all, of the species: 1) Strong aggressiveness; 2) Irregular arrangement of batches (14); 3) Readiness to prepare a wax envelope (17); 4) Frequent nectar stealing (20); 5) Large colony size (26); 6) Large size difference

between queens and workers (21). The peculiarity of this subgenus has often been overlooked, perhaps hidden by the emphasis on the distinction between pocket makers and non-pocket makers. But it seems to occupy rather an isolated position among bumblebees. The isozyme study by Stephen et al. (1969) also supports this idea. It may be worthwhile to test how the elaborate caste determination mechanism confirmed in *Bo. terrestris* (21) is distributed within *Bombus* s. str. and throughout the other subgenera.

Among other subgenera, *Thoracobombus* seems uniform in certain characters. All so far bionomically studied species are basically surface nesters. Their colonies are relatively small, batches are rather neatly arranged, and queens and workers are continuous in size. On the other hand, *Pyrobombus*, the largest subgenus, is rather diversified in many bionomic characters. The bionomic diversity of the Nearctic species of this subgenus recognized from various studies, notably by Hobbs (1967) and K.W. Richards (1975), might be interpreted in part as an adaptive radiation in connection with the absence of some Palaearctic subgenera there. Interestingly, both European and Nearctic species of *Subterraneobombus* resemble in many characters, e.g. large clutch size of the first batch (5. 4.), presence of pollen priming in the later cells (11), poor wax production (18), size continuity between queens and workers (21), and later emergence of post-hibernating queens (26). The bionomic study of the Eurasian species of *Cullumanobombus* is needed. This small relic subgenus has a conspicuously disruptive distribution (Skorikov 1922). Its Nearctic representative, *Cl. rufocinctus*, seems a relatively successful species, but the European species, *Cl. cullumanus*, is rare anywhere.

More comparative information obtained through detailed observations on various species is needed to characterize other subgenera bionomically, even those relatively well studied such as *Pyrobombus*, *Fervidobombus*, *Subterraneobombus* and *Thoracobombus*. Our comparative knowledge is yet insufficient for *Bombus*, *Cullumanobombus*, *Confusibombus*, *Diversobombus*, *Kalobombus*, *Megabombus*, *Rhodobombus* and *Separatobombus*, and few or no reliable studies exist, especially on the intranidal life, on the following subgenera, mostly distributed out of Europe and North America: *Alpigenobombus*, *Coccineobombus*, *Festivobombus*, *Fraternobombus*, *Funebribombus*, *Mendacibombus*, *Orientalibombus*, *Pressibombus*, *Rubicundibombus*, *Rufipedibombus*, *Robustobombus*, *Senexibombus*, *Sibiricobombus* and *Tricornibombus*.

2. Phylogeny and bionomic characters

Until various controversies enumerated in the preceding sections are solved, caution is advised in the use of bionomic characters for phyletic interpretations. Here are given some provisional comments on previous phyletic hypotheses.

First the term "phylogenetic" has occasionally been used inadequately. Some statements such as, "die phylogenetische Mittelstellung der Hummeln an der Basis der sozialen Apiden" (Röseler 1966), or, "die phylogenetische Mittelstellung der Hummeln zwischen der kurzlebigen staatenlosen Einsiedlerbienen und der

perennierenden Staaten der Apiden" (Haas 1966), are correct if interpreted in the evolutionary sense, but can lead to a misunderstanding if it means "phylogenetic position." Independent evolution of eusociality in bumblebees and Apinae (honeybees and stingless bees) is likely (Michener 1974) or fairly probable (Sakagami, unpub.). If this opinion is correct, various aspects of social evolution appeared and have proceeded along two different lines and their comparison must be made cautiously.

Milliron (1961, 1971) proposed a polyphyletic origin of bumblebees. Based upon the structure of legs, he considered that the present day bumblebees evolved from xylocopid and anthophorid stems. The idea was rejected by O.W. Richards (1968) as phantastic. Milliron's hypothesis does not give sufficient and reliable evidence for such a drastic opinion. Even admitting such superficial resemblance to Xylocopinae and Anthophorinae, the basic design of bumblebee morphology including legs is quite homogenous throughout the various groups. If such opinion is permitted, we could even assert a polyphyletic origin of stingless bees, a very compact but, concerning leg structure, highly variable group. Moreover, bumblebees are peculiar among bees by complete degeneration of jugal lobes of hind wings, a feature they share only with Euglossini. If Milliron's hypothesis is valid, we must postulate the loss of jugal lobes occurring twice in his dendrogram, which has no place to receive Euglossini, the group in all probability the closest to bumblebees.

Concerning bionomic characters, the most remarkable feature of bumblebees is rearing of several larvae (excl. *Bombias*) in a distensible cell. Communal rearing is rather a rare event in winged Aculeata, known only in some sphecoid wasps, a few bees (*Megachile*, *Lithurge*, ref. Michener 1974) and allodapine bees. And the distensible cell is a unique invention of bumblebees. If Milliron's interpretation is correct, we must again postulate independent acquisition of distensible cells in two groups, as for jugal lobes. Independent evolution of two sets of features, both very peculiar among bees, seems not probable. On the other hand, a polyphyletic origin of the large eyed *Boopobombus* tendency by Milliron is acceptable as discussed in Disc. 1.

Another, more reasonable "polyphyletic" hypothesis was held by Tkalcú (1972). Supporting the skepticism by Grütte (1935) on the origin of parasitic Aculeata from non-parasitic relatives, Tkalcú thought that many parasitic groups have retained the features of undifferentiated pre-parasitic ancestors, from which recent non-parasitic groups evolved. For *Bombus* s. lat. and *Psithyrus*, he assumes secondary derivation of recent bumblebee groups from several stocks, the ancestral features of which are kept by several *Psithyrus* groups.

This interpretation is not impossible. It is really a monophyletism and needs not postulate the polyphyly of a distensible brood cell. But the basis of his interpretation, the absence of unspecialized parasitic groups, or its universal validity, requires further critical studies, especially after the recent discovery of some poorly specialized parasitic species in allodapine and halictine bees (Michener

1974), to which *Al. hyperboreus* and possibly *Th. inexpectatus* described by himself may be added. Anyhow, closer comparative studies of both morphological and bionomic characters are still required to clarify the phyletic relation of various bumblebee groups. Tkalcû proposed a classification of the Eastern genera and subgenera of bumblebees, in part on the basis of host-parasite correspondence between *Bombus* (s. lat.) and *Psithyrus*. But some Nearctic subgenera of *Psithyrus* invade nests of many subgenera of bumblebees (cf. Michener 1974).

3. Evolutionary interpretations of some bionomic characters

Considering habitat preference and some bionomic characters, Postner (1952) divided the species inhabiting Erlangen and the vicinity into two alternative groups: One group is eremophilous (cf. 1) to intermediary in habitat preference, mainly nesting in underground cavities, batch arrangement primitive, colony large and appearance of post-hibernating queens early (Cf. *confusus*, *Bo. terrestris*, *Mg. ruderatus*, *Ml. lapidarius*, *Th. sylvarum*). Another is hylophilous, mainly nesting on surface, batch arrangement complicated, colony small and appearance of post-hibernating queens late (*Bo. lucorum*, *Mg. hortorum*, *Pr. hypnorum*, *pratorum*, *Th. humilis*, *pascuorum*).

First Postner stressed the fact that complicated batch arrangement (Types III~V by Weyrauch, cf. 14) occurs in surface nesters and postulated an increased adaptation of various species from eurytopic-eremophilous via hypereurytopic-intermediary to eurytopic-hylophilous habitat preference. Thereafter, he pointed out quite different habits exhibited by closely allied species and suggested polyphyletic evolution contrary to monophyletism shown by the relation between habitat preference and batch arrangement.

Apart from a confusion between phyletic and evolutionary interpretations (cf. Disc. 2), his bionomic classification seems to contradict observations by other European specialists. Even though the result obtained in and near Erlangen would support his sorting, *Bo. lucorum* could hardly be classified into the second group in all four characters. The position given for *Mg. hortorum* and *Th. sylvarum* is also suspicious. His "monophyletic" interpretation postulates the later derivation of surface nesting from underground nesting. In most winged social insects, underground nesting is regarded as a secondary acquisition. Inability of bumblebees at self excavation except for the formation of hibernacula and enlargement of pre-existing subterranean cavities favors the secondary nature of underground nesting. Four characters and habitat preference adopted by Postner vary among closely related species, i.e., these are characters that are interesting from the evolutionary viewpoint but not phyletically.

The hypothesis by Brian (1957) on the evolution of certain flower visiting habits was commented upon 20. Her opinion is implicit in the sense that the long tongued species evolved by their "psychological" conservatism, i.e., they did not simply develop a long glossa, but by the consequence of their incompatibility with more opportunistic species, which kept relatively short glossa. Possibly this

could explain a superficially paradoxical combination of two characters kept by *Odontobombus* (cf. Disc. 1). One is probably primitive and another specialized, i.e. mass provisioning and elongate glossa. Possibly this interpretation is useful to explain the evolution of Euglossini, the glossa of which is incomparably longer.

Nextly "the generic behavior" proposed by Haas (1962, '65, '66) requires brief comments. First the ambiguity of his term must be mentioned. He defined "das generische Verhalten" as "das Verhalten offenbart werden der Verhaltenselemente des Genus im weitesten Sinne (1962)" or "das Verhalten, das in dem Elemente verschiedener Arten eines Genus offenbart werden (1965)". The second definition is somewhat unclear and by the first definition anyone imagines generic characters, i.e. the characters simply common to all species of the genus (cf. p. 401, foot note). But he uses the term for the allochthonous appearance of behavior possessed by other congeneric species (of bumblebees) or by solitary bees or other apid bees (honeybees and stingless bees). To avoid possible confusion, the terms allospecific or allogeneric behavior should be used for the latter case.

Secondly, he considers that bumblebees are "arttypisch nicht durchdifferenziert", by their phylogenetic intermediate position between solitary bees and apids with perennial colonies. That bumblebees occupy an intermediate position is correct in the evolutionary sense but not always phylogenetically (cf. Disc. 2). Further, such an intermediate position may not necessarily result in behavioral instability.

His interpretations of particular instances (cf. 12. 6., 17) are interesting. But his schematic presentation of the "phylogenetic" development of brood rearing behavior in Apidae (1962, Fig. 13) ignores some important facts: 1) Possible evolution of eusociality in bumblebees independent from that of honeybees and stingless bees (cf. Disc. 2); 2) Communal brood rearing in distensible cells, a unique invention by bumblebees (cf. Disc. 2); 3) Building and utilization of cells by honeybees as in social wasps, being unique among all bees (cf. 16); 4) The extremely differentiated oviposition in stingless bees, being very different from that of any other bees (Sakagami and Zucchi 1974). Certainly bumblebees represent an evolutionary summit of brood rearing behavior, not an intermediate type between solitary bees and Apinae. The unit cell system by mass provisioning, i.e. repetition of cell building - provisioning - oviposition - sealing, which is prevalent in solitary bees, must be the ancestral type, from which three social groups radiated with their own peculiarities.

Based upon extensive studies with the species in Alberta, Hobbs (1964a, cf. 1964b~1968) considered the evolution of brood rearing habits. He regards feeding through a pocket as more primitive than direct feeding (P_1 , all broods fed through pockets; P_2 , only workers fed through pockets; P_3 , direct feeding but pollen cylinder attached to the brood cell; P_4 , direct feeding), pollen priming (R_1) on the bottom of the second and subsequent cells as more primitive than its absence (R_2), and batched oviposition (B_1) as more primitive than individual oviposition (B_2) (cf. 12, 11, 10, respectively). From these interpretations, he derived the

following evolutionary trends among various subgenera:

	P	B	R
<i>Subterraneobombus</i>	1	1	1
<i>Alpinobombus</i> , <i>Fervidobombus</i>	2	2?	1
<i>Pyrobombus</i>	4	1 or 2	1
<i>Cullumanobombus</i>	3	2	1
<i>Bombus</i>	4	2	1
<i>Bombias</i>	4	2	2

Hobbs writes: "The species of *Bombias* could be considered the most advanced because they feed all larvae individually and rear all but the first broods (=the first batch in the present paper) in unprimed cells and therefore more closely resemble species of the genus *Apis*." His interpretations of characters P and R could be correct to judge by a trend in Aculeata, the change from mass provisioning to progressive provisioning, though it must be mentioned that the preparation of a feeding pocket is itself a specialization not found in any other bees. His interpretation of character B is not immune from criticism, because collective rearing with distensible cells of bumblebees is unique (cf. Disc. 2) among Aculeata, apparently indicating a secondary acquisition. Euglossine bees, the closest relative of bumblebees, retain individual rearing with fixed cells (Zucchi et al. 1968). Hence, two alternate interpretations are possible: 1. *Bombias* returned from collective to individual rearing, 2. *Bombias* retained individual rearing after acquisition of distensible cells by ancestral stock, irrespective of its probable specialization in other characters. The opinion by Hobbs becomes valid only after disproving the second alternative. His assertion on the resemblance of *Bombias* to honeybees is superficial, because honeybees are unique among all bee groups by the possession of a cell system shared with social wasps (synchronous building, oviposition in incomplete cells, reuse of cells), possibly acquired with the adoption of hanging combs.

Finally an interesting hypothesis by K.W. Richards (1975) is referred to. From various surveys of the Alberta species, he argued the occurrence of two different strategies in colony growth. One is taken by earlier nest establishing species (cf. 26). They have fewer worker immatures in the first batch, but produce subsequently a large number of workers and many sexuals per colony. The number of workers necessary to produce each sexual is large. Another is employed by later establishing species, with a larger number of worker immatures in the first batch, a smaller number of subsequently produced workers (exception, *Cl. rufocinctus*) as well as sexuals. The number of workers required for each sexual is small. From the efficiency of colony productivity, the second type is superior, but "excess" workers in the first type may be useful for defense and maximizing foraging activities in favorable periods.

Apparently these alternate strategies, with possible intermediary ones, may have evolved independently in various subgenera. At the same time, however, it is possible that some subgenera tend to one of them. Various bionomic characters

enumerated in the present review must vary in their plasticity, from relatively fixed ones such as presence or absence of feeding pockets to presumably more plastic ones such as flower preference, easily modified by environmental conditions. Life modes of various bumblebee species are superficially similar, but actually are woven by these numerous characters. The present paper certainly does not add even a single item of new information to previous knowledge. Yet I hope that it serves in some way for the advance of bumblebee bionomics.

Summary

Previous records on the specific differences in bionomic characters of various bumblebee species were reviewed and discussed for 28 items. Some evolutionary and phyletic interpretations were reviewed. Some of the recorded differences seem really species or group specific, but many are obscured by careless records and controversial observations. The necessity of accumulating more precise and standardized records is stressed.

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