“The Ants.”, for *Teleutomyrmex*.

Here follows an extraction from Hölldobler, B. K., Wilson, E. O., 1990, “The Ants.” Cambridge, Mass., Harvard University Press. It is a part from Chapter 12: “Symbioses among ant species.”

“The “ultimate” social parasite.”.

“There is no better way to begin a survey of the social symbioses than by considering the most extreme example known, that of the “ultimate” parasitic ant *Teleutomyrmex schneideri*. This remarkable species was discovered by Heinrich Kutter (1950a) at Saas-Fee, in an isolated valley of the Swiss Alps near Zermatt. Its behavior has been studied by Stumper (1950) and Kutter (1969), its neuroanatomy by Brun (1952), and its general anatomy and histology by Gösswald (1953). A second population has been reported from near Briançon in the French Alps by Collingwood (1956), a third in the French Pyrenees by Buschinger (1987c), and still others in the Spanish Sierra Nevada by Tinaut Ranera (1981). Appropriately, the name *Teleutomyrmex* means “final ant.” The populations of *Teleutomyrmex schneideri*, like those of most workerless parasitic ant species (Wilson, 1963), are small and isolated. The Swiss population appears to be limited to the eastern slope of the Saas Valley, in *Juniper-Arctostaphylos* woodland ranging from 1,800 to 2,300 m in elevation. The ground is covered by thick leaf litter and sprinkled with rocks of various sizes, providing, in short, an ideal environment for ants. The ant fauna is of a typically boreal European complexion, comprising the following free-living species listed in the order of their abundance (Stumper, 1950): *Formica fusca*, *Formica lugubris*, *Tetramorium caespitum*, *Leptothorax acervorum*, *Leptothorax tuberum*, *Camponotus ligniperda*, *Myrmica lobicornis*, *Myrmica sulcinodis*, *Camponotus herculeanus*, *Formica sanguinea*, *Formica rufibarbis*, *Formica pressilabris*, and *Manica rubida*. For some unexplained reason this little assemblage is extremely prone to social parasitism. *Formica sanguinea* is a facultative slavemaking species, preying on the other species of *Formica*. *Doronomyrmex pacis*, a workerless parasite living with *Leptothorax acervorum*, was discovered by Kutter as a genus new to science in the Saas-Fee forest in 1945. In addition, Kutter and Stumper found *Epimyrma stumperi* in nests of *Leptothorax tuberum*, as well as two parasitic *Leptothorax*, *goesswaldi* and *kutteri*, in nests of *Leptothorax acervorum* (Kutter, 1969).”

“*Teleutomyrmex schneideri* is a parasite of *Tetramorium caespitum* and *Tetramorium impurum*. Like so many other social parasites, it is phylogenetically closer to its host than to any of the other members of the ant fauna to which it belongs. In fact, it may have been derived directly from a temporarily freeliving offshoot of this species, since *Tetramorium caespitum* and *Tetramorium impurum* (the host species at Briançon and in the Pyrenees) are the only nonparasitic Tetramoriines known to exist at the present time through most of central Europe. It is difficult to conceive of a stage of social parasitism more advanced than that actually reached by *Teleutomyrmex schneideri*. The species occurs only in the nests of its hosts. It lacks a worker caste, and the queens contribute in no visibly productive way to the economy of the host colonies. The queens are tiny compared with most ants, especially other tetramoriines; they average only about 2,5 mm in total length. They are unique among all known social insects in being ectoparasitic. In other words, they spend much of their time riding on the backs of their hosts. The *Teleutomyrmex* queens display several striking morphological features that are correlated with this peculiar habit. The ventral surface of the gaster (the large terminal part of the body) is strongly concave, permitting the parasites to press their bodies close to those of their hosts. The tarsal claws and arolia are unusually large, permitting the parasites to secure a strong grip on the smooth chitinous body surface of the hosts. The queens have a marked tendency to grasp objects. Given a choice, they will position themselves on the top of the body of the host queen, either on the thorax or the abdomen. Deprived of the nest queen, they will then seize a virgin *Tetramorium* queen, or a worker, or a pupa, or even a dead queen or worker. Stumper observed a case in which six to eight *Teleutomyrmex* queens simultaneously grasped one *Tetramorium* queen, completely immobilizing her. The mode of feeding of the *Teleutomyrmex* is not

known with certainty. The adults are evidently either fed by the host workers through direct regurgitation or else share in the liquid regurgitated to the host queen. In any case, they are almost completely inactive most of the time. The *Teleutomyrmex* adults, especially the older queens, are highly attractive to the host workers, who lick them frequently. According to Gösswald, large numbers of unicellular glands are located just under the cuticle of the thorax, pedicel, and abdomen of the queens; these are associated with glandular hairs and are believed to be the source of a special attractant for the host workers. The abdomens of older *Teleutomyrmex* queens become swollen with fat body and ovarioles. This physogastry is made possible by the fact that the intersegmental membranes are thicker and more sclerotized than is usually the case in ant queens and can therefore be stretched more. Also, the abdominal sclerites themselves are widely overlapping in the virgin queen, so that the abdomen can be distended to an unusual degree before the sclerites are pulled apart. The ovarioles increase enormously in length, discard their initial orientation, and infiltrate the entire abdomen and even the postpetiolar cavity."

"From one to several physogastric queens are found in each parasitized nest, usually riding on the back of the host queen. Each lays an average of one egg every thirty seconds. The infested *Tetramorium* colonies are typically smaller than uninfested ones, but they still contain up to several thousand workers. The *Tetramorium* queens also lay eggs, and these are capable of developing into either workers or sexual forms (Buschinger, personal communication). Consequently the brood of a parasitized colony consists typically of eggs, larvae, and pupae of *Teleutomyrmex* queens and males mixed with those of *Tetramorium* workers."

"The bodies of the *Teleutomyrmex* queens bear the mark of extensive morphological degeneration correlated with their loss of social functions. The labial and postpharyngeal glands are reduced, and the maxillary and metapleural glands are completely absent. The mandibular glands, on the other hand, are apparently normal. In addition, the queens possess a tibial gland, the function of which is unknown. The integument is thin and less pigmented and sculptured in comparison with that of *Tetramorium*; as a result of these reductions the queens are shining brown, an appearance that contrasts with the opaque blackish brown of their hosts. The sting and poison apparatus are reduced; the mandibles are so degenerate that the parasites are probably unable to secure food on their own; the tibial-tarsal cleaning apparatus is underdeveloped; and, of even greater interest, the brain is reduced in size with visible degeneration in the associative centers. In the central nerve cord, ganglia 9-13 are fused into a single piece. The males are also degenerate. Their bodies, like those of the males of a few other extreme social parasites, are "pupoïd," meaning that the cuticle is thin and depigmented, actually greyish in color; the petiole and postpetiole are thick and provided with broad articulating surfaces; and the abdomen is soft and deflected downward at the tip."

The *Teleutomyrmex*-male has, contrary to other extreme, workerless inquiline males, "reduced", non-functional wings, so, no more nuptial flights! The other species have no wings.

"In its essentials the life cycle of *Teleutomyrmex schneideri* resembles that of other known extreme ant parasites. Mating takes place within the host nest. The fecundated queens then either shed their wings and join the small force of egg layers within the home nest or else fly out in search of new *Tetramorium* nests to infest. Stumper found that the queens could be transferred readily from one *Tetramorium* colony to another, provided the recipient colony originated from the Saas-Fee. However, *Tetramorium* colonies from Luxembourg were hostile to the little parasites. Less surprisingly, ant species from the Saas-Fee other than *Tetramorium caespitum* always rejected the *Teleutomyrmex*. However, Buschinger (personal communication) has pointed out that the Saas-Fee population could be *caespitum* or *impurum*, or a mixture of both. In other words, the transfer might have been attempted across species."

“Tinaut, A., 1990.”, for *Teleutomyrmex kutteri*.

“Biotope.”

“This species has been found in a mountain brushwood, which is mainly comprised of *Juniperus communis* and *Genista baetica*, included in the Oro-mediterranean level. In this biotope, the following species of free-living Formicidae with bracketed percentages of abundance are found: *Tetramorium caespitum* (Linnaeus, 1758) (11.54), *Leptothorax tuberum* (Fabricius, 1775) (1.75), *Tapinoma nigerrimun f* (Nylander, 1886) (62.24), *Proformica longiseta* Collingwood, 1978 (23.08), and *Lasius flavus* (Fabricius, 1781) (1.39). Among parasitic species, we found: *Strongylognatus testaceus* (Schenk, 1852) and *S.* prope *caecıliae* Forel, 1897.”

“As host species we found only *T. caespitum* (Linnaeus, 1758), even though Buschinger (1985, 1987) refers to *T. impurum* (Foerster, 1850) as the host in the nests found by him at Briançon and in the Pyrenees, respectively.”

“According to Lopez (1988), identification and status of *T. impurum* ın Spain ist not clear, not even when studying the males; in our case, all males found in the area in which *Teleutomyrmex* was discovered correspond to *T. caespitum*.”

“Kiran, K., Karaman, C., Lapeva-Gjonova, A., Aksoy, V., 2017.”, for *Teleutomyrmex*.

From **the introduction**:

“*Teleutomyrmex* was first described by Kutter (1950) from Switzerland, with the generic name meaning "final ant". Members of the genus are known as ectoparasites spending most of their time riding particularly on mesosoma or abdomen of their host queens. This uncommon habit of *Teleutomyrmex* queens in host nests led to the development of some special morphological characters – i.e., a strongly concave ventral surface of an extremely flattened gaster, very large tarsal claws, and huge arolia allowing tight adhesion on glabrous surfaces of the host queen.”

“*Teleutomyrmex schneideri* and *T. kutteri* Tinaut, 1990 are the two species of the genus *Teleutomyrmex* known so far. After the first record of *T. schneideri* from Switzerland (Kutter 1950, Stumper 1951), Collingwood (1956), Buschinger (1985, 1987, 1999), Espadaler & Cuesta (2006) and Wegnez & al. (2015) recorded this species from the Swiss Alps (Saas Fee, Simplon), the French Alps (Briançon, Vallée de la Maurienne) and the French Pyrenees (Vallée d'Ossau). The studies of Kutter (1950), Brun (1952), Gösswald (1953), and Cuesta & al. (2009) provided additional data on biology and anatomy of the species. A *Teleutomyrmex* finding from Farap (previously: Farab) in Turkmenistan was attributed by Dlussky & al. (1990) to *T. schneideri*. Yet, considering the weak dispersal capacity of *Teleutomyrmex* in general and specifically the comparably cold thermal niche of *T. schneideri* with habitats in the upper montane and alpine zone of the Alps, it is difficult to believe that a finding in a hot Middle Asian lowland desert some 4500 km east of Switzerland should refer to the same species.”

“Tinaut (1990) described a second species, *Teleutomyrmex kutteri*, from the Sierra Nevada in Spain which differs mainly by hair length on propodeum and petiole, and genitals of males. *Teleutomyrmex kutteri* was recently recorded in Cazorla, La Empanada (Spain, Andalucia) (Lôpez & Martinez 2011).”

“Ward & al. (2015) proposed to synonymize the ant genera *Teleutomyrmex* Kutter, 1950, *Rhoptromyrmex* Mayr, 1901, and *Anergates* Forel, 1874 with *Tetramorium* Mayr, 1855 which, as a consequence, would become a mega-genus containing over 450 described species. This extreme decision would mean that both species of *Teleutomyrmex* would fall into secondary homonymy.

Teleutomyrmex schneideri Kutter, 1950 would become a junior secondary homonym of *Tetramorium schneideri* Emery, 1898; accordingly, Ward & al. (2015) proposed to replace the name *Tetramorium schneideri* Kutter with *Tetramorium inquilinum* Ward, Brady, Fisher & Schultz, 2015. Yet, they overlooked that *Tetramorium kutteri* Tinayt, 1990 would also become a junior secondary homonym of *Tetramorium semilaeve* var. *kutteri* Santschi, 1927 if their concept would be accepted. We do not follow here the proposals of Ward & al. (2015). The mega-genus *Tetramorium* in the conception of Ward & al. (2015) refers to a big clade of myrmecine ants collecting at least eight subclades under a single name but each of these morphologically (and apparently also genetically – see Ward & al. 2015: fig. 1) well-defined subclades deserves to have a genus name on its own. Combining well-differentiated clades with most different life histories under a single name would make communication between recent and future myrmecologists extremely cumbersome and confusing. Seifert & al. (2016) presented three lines of argumentation under which conditions paraphyletic clades deserve a genus name. The most important of their arguments was perhaps saving the functionality of scientific language. Yet, the expectable subdivision of the mega-genus *Tetramorium* sensu Ward & al. (2015) into at least eight monophyletic subclades with each potentially deserving a genus rank makes a paraphyly discussion not necessary in this case."

From **the description of *Teleutomyrmex seiferti***:

"Ecology: The type series was collected from a *Tetramorium* cf. *chefketi* nest located under a stone in a *Pinus sylvestris* L. forest older than 100 years. There are many trees about to die because of their old age, and therefore there are very large sun exposed areas on the forest ground. The ground is not inclined near the nest because the nest site is placed on the top of the hill."

"The habitat is similar to that reported by Tinaut (1990) for the type locality of *Teleutomyrmex kutteri*. Herb layer plants of the forest ground consist mainly of *Astragalus* sp., *Hieracium* sp., *Thymus* sp., *Pilosella* sp., *Ajuga* sp., *Centaurea* sp., *Juniperus communis* L., and *Stipa* sp. The following 14 ant species were recorded from the type locality: *Camponotus aethiops* (Latreille, 1798), *C. piceus* (Leach, 1825), *Cataglyphis aenescens* (Nylander, 1849), *Crematogaster schmidti* (Mayr, 1853), *Formica clara* Forel, 1886, *F. cunicularia* Latreille, 1798, *Lasius alienus* (Förster, 1850), *Messor structor* (Latrelle, 1798), *Proformica striaticeps* (Forel, 1911), *Tapinoma* cf. *simrothi* Krausse-Heldrungen, 1911, *Temnothorax interruptus* (Schenck, 1852), *Tetramorium* cf. *caespitum* (Linnaeus, 1758), *T. ferox* Ruzsky, 1903, *T. moravicum* Kratochvil, 1941. The long-term average of mean air temperature in 2 m height from 1 May to 31 August TAS is 11.3 °C." at "1801 m above sea level."

From **the description of *Teleutomyrmex buschingeri***:

"Ecology: The nest of *Tetramorium* cf. *chefketi* with *Teleutomyrmex buschingeri* sp.n. was found under a stone on a southern slope of a dry grassland situated in an oak forest. The habitat type is quite different from the known habitats of related species. The altitude of 640 m, where the species was sampled, is notably less than the altitudes of the localities of the other ultimate ant parasites (1600 - 2300 m) (excluding the one in Turkmenistan.)."

"The following 21 ant species were recorded in the same area: *Bothriomyrmex corsicus* Santschi, 1923, *Camponotus aethiops*, *C. piceus*, *C. samius* Forel, 1889, *Cataglyphis nodus* (Brullé, 1883), *Formica cunicularia*, *F. gagates* Latreille, 1798, *Lasius* cf. *distinguendus* (Emery, 1916), *L. psammophilus* Seifert, 1992, *Messor structor*, *Myrmica specioides* Bondroit, 1918, *Pheidole* cf.*pallidula* (Nylander, 1849), *Plagiolepis pygmaea* (Latreille, 1798), *Ponera testacea* Emery, 1895, *Solenopsis fugax* (Latreille, 1798), *Tapinoma erraticum* (Latreille, 1798), *Temnothorax parvulus* (Schenck, 1852), *T. semiruber* (André, 1881), *Tetramorium hungaricum* Röszler, 1935, *T. indocile* Santschi, 1927, and *T. moravicum*. The ant community is mainly composed by xerothermophilous species preferring warm and sunny areas. The Eastern Rhodopes have low and hilly landscape with

an average altitude of 320 m and the highest point is 1483 m. Continental-Mediterranean climate determines the relatively high average annual temperature of 12 °C and the mean longterm air temperature in 2 m height from 1 May to 31 August TAS is 18.0 °C." at "640 m a.s.l."

And in **the discussion** they come back:

"The data presented above justify the separation of four *Teleutomyrmex* species – this is a surprising species richness for such an extremely evolved ant genus. Even more, this story is most certainly incomplete: The existence of a fifth, undescribed species from Middle Asia is most probable. A finding at the locality Farab (the former Farap, 39.15° N, 63.61° E, 190 m a.s.l.) in Turkmenistan made in 1988, is most unlikely to belong to *T. schneideri* under which name it has been published by Dlussky & al. (1990). Farab is 4500 km distant from the next site of *T. schneideri* in Switzerland and the climatic and faunistic context of this site situated in a river plane at the margin of the Kara-Kum desert is dramatically different: TAS in Farab is 35.0 °C and the *Tetramorium* species occurring there (Dlussky 1981) are different from the known host species of the described *Teleutomyrmex* species."