SUPERSPECIES *PYRGUS MALVAE* (LEPIDOPTERA: HESPERIIDAE) IN THE EAST MEDITERRANEAN, WITH NOTES ON PHYLOGENETIC AND BIOLOGICAL RELATIONSHIPS

by

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The possible zone of contact between *Pyrgus (malvae) malvae* Linnaeus, 1758, and *P. (malvae) melotis* Duponchel, 1832, is re-examined. The two taxa apparently meet (in the subspecies *malvae* and *ponticus* Reverdin, 1914, respectively) in N. and W. Turkey and possibly in S. Russia north of the Caucasus. There are, however, only few localities or areas from where both are known: Amasya and north of Ankara in N. Turkey and Izmir in W. Turkey. In these areas the two taxa do not seem to recognize each other as belonging to the same species. A population with an intermediate character is known to occur in the Boz Dagh area east of Izmir. The population seems remarkably constant in this character. Its origin is obscure. The available data do not prompt us to change our view on the superspecies status of *Pyrgus (malvae)*. Notes are added on the apparent incongruence of phylogenetic and biological relationships in this case. *P. (malvae) melotis* is widely distributed in Turkey, extending east to N. Iran, north to north of the Caucasus and south to Israel. Old records of *melotis* from Greece or the Aegean islands are highly improbable and should be omitted from further literature records. On the basis of external characters two subspecies are distinguished: *melotis* and *ponticus*.


CONTEXT OF THE PROBLEM

The genus *Pyrgus* Hübner as currently conceived is remarkable for the relatively large number of cases of partly incomplete or apparently just completed speciation. In the New World there are the cases of *P. limbatus-barrosi*, *P. scriptura-xanthus* and *P. communis-albescens*, in the Old World *P. obertuieri-dejeani-nepalensis*, *P. alpinus-cashmirensis-darwazicus*, *P. carolinae-cirsii*, *P. malvae-malvoides-melotis* and the *P. alveus* complex. Appar-
ently evolution is quite active in this genus. In some cases partially successful interbreeding is known at a scale that may very locally. It makes it difficult to assign a particular taxonomic rank to the populations involved. As a consequence opinions vary widely as to what should be considered “still” conspecific or “no longer” conspecific. The theoretical aspect of this kind of situation is interesting and can deepen our insight in evolutionary processes. The practical problem of the taxonomic rank, however, is annoying and can only be solved by consensus of opinions.

THE CASE OF *PYRGUS MALVAE*

To distinguish various degrees of advancement in speciation several terms are in use such as “species group”, “species complex”, and “superspecies”. In 1972 I distinguished a superspecies *Pyrgus malvae* (Linnaeus, 1758) with as semispecies *P. (malvae) malvae*, *P. (malvae) malvoides* (Elwes & Edwards, 1897) and *P. (malvae) melotis* (Duponchel, 1832). This division was followed by Guillaumin & Descimon (1976) who thoroughly studied the species concept in Lepidoptera. In some popular handbooks like Higgins (1975) and Higgins & Riley (1980) only a “normal” species *P. malvae* with four subspecies (*malvae, malvoides, melotis, ponticus*) is recognized, but this is certainly not an optimal representation of the known facts. The situation in superspecies *Pyrgus malvae* can be summarized as follows.

![Diagram of distribution](image)

**Fig. 1.** Distribution of *Pyrgus (malvae) malvae* (1), *P. (m.) malvoides* (2), and *P. (m.) melotis* (3).
The superspecies is distributed all over the Palaeartic Region from the British Isles to Japan and from Scandinavia to the Mediterranean (fig. 1). Over this wide area there is a marked geographic variation in male and female genitalia, and three types, coinciding with the subdivision into semispecies, can be distinguished (figs. 2-4) (terminology according to De Jong, 1972, 1978):

1. *malvae* type – Male: uncus completely split into two diverging parts; gnathos with basal part smoothly curving close to tegumen, suddenly curving distad where tegumen narrows into vinculum, from here with a long up and again downcurving, spined process larger than basal part of gnathos, and with a rather narrow ventral, sclerotized band, which medially bears short, knob-like spines (“ventral plate”); cucullus with pointed apex; costal process without distinctive stylus or antistylus, the former represented by a distad pointing apex, the latter completely absent or represented by a short point. Female: a large genital plate, which is completely split into two parts or indented to middle, basal edge straight or indented medially.

2. *malvoides* type – Male: uncus entire, sometimes a very narrow slit at apex; gnathos with short, straight projection pointing distad instead of the long curved projection of the *malvae* type, ventral band smooth; cucullus rounded at apex; costal process with distinctive stylus and antistylus. Female: a large genital plate with rather narrow V-shaped apical indentation to 1/4-1/3 of length of plate, basal edge more or less straight.

3. *melotis* type – Male: uncus as in *malvoides* type; gnathos with the large curved processes of the *malvae* type but smooth (at most a single tooth close to tip), moreover with much shorter, pointed, straight or curved processes flanking the smooth ventral plate; cucullus and costal process similar in outline to *malvoides* type. Female: a large genital plate with a wide V-shaped apical cleft and with lateral parts further extending basad than medial part.

Roughly the distribution of the three types is as follows (fig. 1). The *malvoides* type is restricted to SW. Europe, the *melotis* type occurs in Turkey and the Near East, while the *malvae* type has a trans-Palaeartic distribution occurring from England to Japan (Hokkaido). The contact zone of the *malvae* and *malvoides* types in Central France was extensively studied by Guillaumin (1971, 1974) who found a locally differing degree of interbreeding indicating that the two types to some degree still can recognize each other as belonging to the same species.
The contact zone of the *malvae* and *melotis* types has never been the subject of such a detailed study. Both types were recorded from Turkey by Evans (1949), Higgins (1966) and Warren (1926), but localities were far apart and it remained uncertain whether the two types really came into contact. The most recent review of the situation was given by De Jong (1972), be it in a rather generalized way. It is 15 years later now and many new collections have been made in Turkey in recent years. Although new data on the superspecies are
remarkably few it seems time to give a detailed description of the present state of knowledge. This may indicate the gaps in our knowledge and prompt people to fill the gaps.

VARIATION OF PYRGUS (MALVAE) MALVAE AND P. (MALVAE) MELOTIS

Each of the three semispecies varies geographically. The variation of P. (malvae) malvoides is not relevant here, for this see De Jong (1972).

Pyrgus (malvae) malvae

The variation of P. (malvae) malvae concerns the male and female genitalia. There is also some variation in external characters but this is not geographical. The genitalic variation divides the semispecies into two subspecies: malvae Linnaeus, 1758 (figs. 5, 11), occurring from England to E. Asia, and kauffmanni Alberti, 1955 (= coreanus Warren, 1957), restricted to the Amur Region, Korea and N. Japan (Hokkaido). There is a large transition area in Transbaikalia (see De Jong, 1972; Warren, 1957). The male genitalia of ssp. malvae are reduced in length and increased in depth compared with ssp. kauffmanni. In both subspecies the uncus is completely split into two elongate, divergent pieces, but while the articulation of the parts is at right angles to the central line of the tegumen in ssp. kauffmanni, the parts are set more obliquely in ssp. malvae so that in lateral view the parts do not cover each other completely. In the female genitalia, the genital plate is completely divided into two parts and the ductus bursae normally membranous in ssp. malvae, while in ssp. kauffmanni the genital plate, though deeply incised, is entire, and the ductus bursae sclerotized.

Pyrgus (malvae) melotis

In P. (malvae) melotis there is a marked variation in the external characters and two subspecies can be distinguished on the basis of these characters: (figs. 7-10, 13-16):

a) ssp. melotis Duponchel, 1832, occurring from Israel and Jordan north to southern Turkey; it is relatively large (length of forewing 11-15 mm) and characterized by the underside of the hindwing, which is cream-coloured obscuring the markings; the spots on the upperside, especially those of the forewing, are generally large and square;
Figs. 5-10. Variation in superspecies *Pyrgus malvae*. 5, *P. (m.) malvae malvae*, The Netherlands; 6, *P. (m.) melotis graecus*, Boz Dagh (W. Turkey); 7, *P. (m.) melotis ponticus*, Adana (S. Turkey); 8, *P. (m.) melotis ponticus*, Novorossiysk; 9, *P. (m.) melotis ponticus*, Hakkari (S.E. Turkey); 10, *P. (m.) melotis melotis*, Lebanon.

b) ssp. *ponticus* Reverdin, 1914, occurring in Turkey, N. Iran, the Caucasus and Transcaucasia, and north at least as far as Novorossiysk; externally it is indistinguishable from *P. (malvae) malvae*; length of forewing, 10-12.5 (-14) mm.

In the province of Hakkari in the extreme South-East of Turkey specimens are characterized by large spots, particularly prominent on the upperside of the hindwing, where they are larger, more complete and more sharply defined than in specimens from elsewhere; on the underside of the hindwing the spots
are also large and well contrasting with the ground colour, which is often darkened by an intermingling of black scales. On the average the specimens are larger than usual for ssp. ponticus, about the size of ssp. melotis, length of forewing 11.0-13.6 mm. The large spots are sometimes found in exceptional individuals from areas outside Hakkari, as far as the province of Kars. Similarly, not every specimen from Hakkari has the spots developed to the same degree.

Dr. Wagener kindly informed me that in many other species of butterflies a similar pattern of geographic variation occurs. The main cause seems to be the exceptional orographic and climatic conditions of the area, with high escarp-
ments, very high temperatures and high humidity due to strong evaporation. Possibly the variation is not genetically determined. Rearing experiments with Melanargia have shown that the variation in this genus does not have a hereditary basis (Wagener, pers. comm.). For other butterflies it must yet be proven, but for the time being it does not seem wise to distinguish subspecies in these cases, although the variation may be very striking.

The difference between ssp. melotis and ssp. ponticus is so striking that it is not remarkable that the two have been considered separate species by various authors. In southern Turkey, however, it is difficult to draw a sharp line between the two, the extent and strength of the cream colour on the underside of the hindwing being variable. Moreover, the genitalia are similar.

There is some variation in the male genitalia of P. (malvae) melotis (figs. 17-22), but it seems mainly individual. The ventral spine of the gnathos is straight or slightly curved; it points dorsad in ssp. melotis and sometimes in ssp. ponticus (mainly along the south coast?), but in the latter it usually points distodorsad or distad (towards the apex of the large dorsal gnathos arm). The ventral spine is usually well developed, but especially in the western part of the area it may be reduced and obsolete. There is also variation in the degree of curving of the dorsal extension of the gnathos, but it seems to be individual and not geographical. Going from east to west there seems to be an increase in the development of a dorsal ridge on the dorsal gnathos arm in ssp. ponticus, but it is not yet clear if this is a clinal variation or rather an individual one. The variation in the valves seems to be individual.

No constant difference has been found so far in the female genitalia between the subspecies of this semispecies.

From this description it follows that the possible contact between P. (malvae) malvae and P. (malvae) melotis is between the most extreme form of the former, ssp. malvae, and the externally similar ssp. ponticus of the latter. Because of their external similarity possible hybridization can only be detected by studying the genitalia.

**INTERMEDIATES BETWEEN P. (MALVAE) MALVAE AND P. (MALVAE) MELOTIS**

Since the two semispecies are so different in their genitalia, intermediate specimens should be easily distinguishable, for instance by an incompletely split uncus or an almost divided genital plate. Such specimens, though rare, are
known indeed. Unfortunately the few specimens are not all reliably labelled. I have seen the following material.

1. Greece. In 1910 Oberthür described Syrichtus malvae graeca from Greece. The holotype (♂), now in the BMNH, originally comes from the Bellier collection and is labelled “Grèce”. Externally it is like ssp. malvae and ssp. ponticus, but the genitalia are intermediate (fig. 23): the uncus is split to about 1/3 with the parts diverging, the gnathos has a smooth dorsal arm and practically no ventral spine, the valva is of the meloitis type. There is another
specimen in the BMNH from the Bellier collection, also labelled “Grèce”, which externally and in the genitalia is similar to the holotype of *graeca*, but with the uncus almost split to halfway.

These are the only intermediate specimens from Greece known to me. Surprisingly, there are two more males from the Bellier collection in the BMNH, with identical labels, but with the genitalia of the *malvae* type. There are four other old Greek specimens in the BMNH that belong to ssp. *melotis* according to the genitalia and external characters. All other Greek specimens examined (over 40 specimens from the northern and central part of Greece, south to the Parnassos and Athens) are pure ssp. *malvae*. Also in the Peloponnesos (Mt. Páron, Mr. Taýgetos, Mt. Helmós) only typical ssp. *malvae* is known to occur (Coutsis, pers. comm.). In view of this it is highly unlikely that the two intermediate specimens really originate from Greece. I rather suppose them to come from W. Turkey. It is even more unlikely that the Greek specimens of ssp. *melotis* are correctly labelled, see next chapter.

2. West Turkey. There is a series of 18 ♂ and 2 ♀ from the Boz Dagh, east of Izmir, in the RMNH. The males are all similar to the holotype of *graeca* (figs. 6, 12, 24). The depth of the incision of the uncus varies somewhat, from 1/4 to 1/3, but for the rest it is a remarkably constant series. In the BMNH there is a single male from “Smyrna” (now Izmir) that is similar to the specimens from the Boz Dagh, except that it is a bit paler above and below. Since the specimens are much more similar to *P. (malvae) melotis* than to *P. (malvae) malvae*, they are referred to as *P. (malvae) melotis graecus*.

3. North Turkey. No intermediate specimens are known from N. Turkey, but one male of ssp. *ponticus* in the BMNH from Tokat has the extreme tip of the uncus with a small V-shaped notch. In view of the locality it could imply influence of ssp. *malvae*, but the notch is quite small and could as well be an individual variation.

Apart from these examined specimens there is a literature record by Reverdin (1911) of a specimen of ssp. *melotis* with the uncus bifid more or less as in ssp. *malvae*. Reverdin did not mention the locality, only stressed that it was a curiosity on which no theories about common descent of ssp. *melotis* and ssp. *malvae* could be based.

**DISTRIBUTION OF P. (MALVAE) MELOTIS**

It is at the same time amusing and frustrating to see how easily mistakes are made and maintained in literature. The present taxon provides a striking example. Tutt (1905-1906) gave as distribution of ssp. *melotis*: “It occurs in
May in the Tirol and in Switzerland (Duponchel).” What apparently had happened was that the translator of the original description of *melotis* when come to the end of the page turned over two pages and the intervening plate instead of one, and translated the concluding sentence of Duponchel’s treatise of *Pyrgus alveus* (recte *P. armoricanus*). Rowland-Brown (1912), while explaining this mistake, wrote: “Now *melotis*, or *hypooleucos*, occurs in Andalusia, where Rambur found and described it (Cat. Lepid. And. p. 76, 1858) . . .” Here, Rowland-Brown introduced a new mistake. Perhaps he did not see the original text by Rambur, or he did not understand the French. Fact is that Rambur gave a description of *Pyrgus (malvae) malvoides* from Grenada under the name “*Scelotrix Alveolus*, Hübner” while referring to a figure by himself (Rambur, 1839: pl. 8 fig. 15. r) of *P. (malvae) malvae*. In a footnote he described a specimen from Syria under the name “*Scelotrix Melotis Duponchel*”, synonymizing it with “*Hesperia Hypoleucos Lederer*”, and remarking that Boisduval’s opinion *melotis* would belong to *alveolus* (= *malvae*) was
apparently wrong. Nowhere did he mention its occurrence in Spain.

Warren (1926) copied Rowland-Brown's mistake and added that apart from Andalusia the only reliable record for Europe he could find was Greece, according to the collection of the BMNH. In fact this museum has the only specimens of *melotis* labelled as coming from Greece. There are four specimens: one male and one female labelled "Graecia" and coming from the Groum-Grshimalo collection, one male labelled "Greece" from the Adams Bequest, and one male labelled "Graec." from the Leech collection. The four specimens are pure ssp. *melotis*. Since ssp. *melotis* is else unknown from mainland Greece while there is quite some material of ssp. *malvae* available, Evans (1949) suggested that the four specimens could have come from the Isle of Milos, the southwestern island of the Cyclades and the type-locality of ssp. *melotis*. However, this locality itself is most doubtful and improbable. I don't know of any other records from the Isle of Milos (see also Coutsis, 1985), but since all other specimens of ssp. *melotis* come from the area of S. Turkey to Israel and Jordan, while ssp. *ponticus* occurs from here to the Aegean Sea, the occurrence of ssp. *melotis* in one of the Aegean islands must either be an introduction or be based on mislabelled material. The alternative is that ssp. *melotis* once had a much wider distribution but was pushed away in distant parts by climatic changes or by competitors (ssp. *ponticus*?) while the intervening area was taken over by ssp. *ponticus*. There are no arguments whatsoever in favour of such a sequence of events, and until new material of ssp. *melotis* becomes available from the Isle of Milos, it is safest to consider the distribution of ssp. *melotis* as being restricted to the rather narrow area from S. Turkey (mainly the province of Hatay) to Israel and Jordan.

*P. (malvae) melotis* is widely distributed in Turkey. The northernmost localities known so far are: Izmir, Güvem, Çubuk Baraji, Amasya, Tokat, Gümüşane. It is not known from the northwestern part of Turkey (see below, the distribution of *P. (malvae) malvae*) nor from wide areas in the central part of the country in spite of extensive collections made in recent years. This may be partly due to the flight period being mainly April/May and August, i.e. outside the main collecting season. In fig. 25 the localities in the Asiatic part of Turkey have been indicated of specimens of which I have examined the genitalia. A complete list of all known localities will be provided by Wagener & Hesselbarth in their forthcoming detailed study of the Turkish butterflies.

The semispecies certainly occurs further east (as ssp. *ponticus*). In the NHMW there are a male and a female from Chalus at the Caspian Sea north of Teheran. I have not seen any specimens nor records from the area between Chalus and Turkey (about 600 km), but there is no reason why ssp. *ponticus* should not occur there. Romanoff (1884), while dealing with the lepidopterous
fauna of the Caucasus and Transcaucasia south to the Iranian border recorded “malvae” (undoubtedly = ponticus) as occurring everywhere.

To the northeast ssp. ponticus extends throughout the Caucasus (Alberti, 1969, 1973). It is likely to occur north of the mountain chain as well, but records are wanting except for Novorossiysk (13 ♂, 4 ♀, RMNH; 1 ♂, 1 ♀, BMNH). There are no records known to me from the area between Novorossiysk, Crimea (where P. (malvae) malvae occurs, see Nekrutenko, 1985) and Sarepta (1 ♂, 1 ♀ of P. (malvae) malvae in BMNH).

Mention should be made here of the ssp. caucasica Rjabov of “Pyrgus melotis” mentioned by Korshunov (1972) from the Caucasus in addition to “Pyrgus ponticus”. I have not seen the original description of Rjabov’s caucasica but it seems unlikely that it is different from P. (malvae) melotis ponticus.

**DISTRIBUTION OF P. (MALVAE) MALVAE IN TURKEY**

In spite of intensive collecting in Turkey in recent years the distribution of P. (malvae) malvae in Turkey is still insufficiently known. Possibly this taxon is much scattered and infrequent, but undercollecting of the right areas may also be part of the explanation, most collectors in Turkey going after the more Oriental species and therefore skipping the northwestern part of Asiatic Turkey.
Since in the European part of Turkey only *P. (malvae) malvae* occurs, localities in this area are not listed separately. The localities in the Asiatic part from where I have seen and checked specimens of *P. (malvae) malvae* (BMNH, abbreviated "B", and through courtesy of Dr. Wagener, abbreviated "W") are as follows (see fig. 25):

- **Prov. Istanbul**: Alemdagh, Beykoz (Beilos) (both B), Göktürk (near Kemerburgaz) (W);
- **Prov. Bursa**: Bursa (Brussa) (B);
- **Prov. Izmir**: Bornova (Burnabat) (B);
- **Prov. Bolu**: Abant Gölü (W);
- **Prov. Zonguldak**: Zonguldak (B);
- **Prov. Ankara**: Kızılıcahamam, Çubuk Baraji (ab. tarsas) (both W);
- **Prov. Amasya**: Amasya (Amasia) (B);
- **Prov. Samsun**: Engiz, Çarsamba (easternmost locality for *P. (malvae) malvae* in Turkey) (both B).

Literature records of *P. (malvae) malvae* from Turkey are not reliable if not based on genitalic examination. The only reliable literature record I know of is Merzifon (Mersifan, Prov. Amasya) (Reverdin, 1911). The male and female of this taxon mentioned by De Lattin (1950) from Sivrice actually are ssp. *ponticus*.

**PUTTING IT ALL TOGETHER**

As far as present knowledge goes, *P. (malvae) malvae* and *P. (malvae) melotis* do not meet with the apparent exception of the following areas: İzmir, Çubuk Baraji, Kızılıcahamam-Güvem, Amasya. So far the two taxa have not actually been found together. There are no indications of intergradation except east of İzmir where a population exists that in the genitalia shows the characters of *P. (malvae) melotis ponticus*, but with a trait of *P. (malvae) malvae* (split uncus). The male from Tokat with the shallowly indented apex of the uncus can hardly be considered an example of intergradation as long as more, similar specimens are wanting. From the possible zone of contact north of the Caucasus no material at all is known.

The intermediate material is remarkable for its low degree of variation. The variation mainly concerns the depth of the incision of the uncus (1/4 to 1/3). This relative constancy is the more remarkable considering that the specimens with the incised uncus are in part very old, dating from before 1888 (the year Bellier died; Oberthür who used specimens from the Bellier collection for the
description of his "graeca", acquired this collection in 1889, see Horn & Kahle, 1935), partly quite recent (1965, the Boz Dagh material in RMNH). It is suggestive of a stable population without recent influx of genetic material from either malvae or melotis. It would be interesting to know more about the genetic background of this variety. The fact that the specimens are intermediate in a character does not imply automatically that the intermediate situation originated from hybridization. It is even possible that the specimens belong to a relic population that originally branched off from melotis and eventually led to malvae. However, with the present knowledge we can only speculate on the nature of the intermediate population.

Anyway, it seems that the development of isolating mechanisms has progressed further between malvae and melotis than between malvae and malvoides. This raises two questions, one practical, the other theoretical. The practical question is: how do we translate this situation taxonomically? I still think that the recognition of a superspecies with three semispecies (malvae, malvoides, melotis) is the best representation of the situation. Alternatively, the three taxa could be considered subspecies of a single species, or three "full" species, or they could be distributed over two species (in two different combinations), but none of these alternatives gives a better representation of the known facts than the recognition of a single superspecies.

Fig. 26. Possible cladograms for superspecies Pyrgus malvae. Only apomorphies are indicated (black circles); they are numbered according to the discussion in the text.
The theoretical problem concerns the interrelationship of the taxa and the distribution of apomorphic characters. Whatever their rank, the three taxa apparently form a monophyletic group. Being a three-taxon group they can be interrelated in three ways as in fig. 26. The only criterion to base the selection of one of the cladograms on is the distribution of apomorphic characters, this being the core of Hennig's phylogenetic methodology. Applying the outgroup rule and taking the other Pyrgus species in the Palaearctic as the outgroup (the phylogeny of the genus will be dealt with in a forthcoming paper), a few apomorphies can be distinguished:

1. Uncus bifid: malvae. It is entire in malvoides and melotis, and all other Palaearctic Pyrgus species.
2. Costal process of valva short, more or less rounded-rhomboidal: malvae. In malvoides and melotis and in all other Palaearctic Pyrgus species the costal process is elongate in dorsodistal and ventroproximal direction, generally differentiated into a stylus and antistylus.
3. Genital plate bipartite or very deeply incised: malvae. It is entire in malvoides and melotis and all other Palaearctic Pyrgus species (if present), and if indented the indentation does not reach middle of plate.
4. Gnathos with long, dorsal processes that curve upwards and then distad: malvae and melotis. Such processes do not occur in malvoides or any other Palaearctic Pyrgus species; the teeth on these processes in malvae could be apomorphic, but the lack of these teeth in melotis could also be a loss.
5. Gnathos with ventral spine: melotis. This spine, which does not occur in other Pyrgus species, could be a transformation of the ventral teeth found in malvoides, in which case its absence in malvae could be a loss, or else it could be a de novo development.

So far no autapomorphies have been found for malvoides, but for the present discussion this is not very important. The distribution of the apomorphies only allows the selection of cladogram 26c, if we want to avoid homoplasic characters. The problem here is that malvae and melotis, although biologically (almost?) two species, are closer phylogenetically than malvae and malvoides, which are still capable of hybridization. It is not possible to apply a single species concept in such cases. The theoretical and practical implications were discussed by Bremer & Wanntorp (1979) and Willmann (1983). Although an evolutionary species concept (cf. Wiley, 1981) would seem to offer a solution, it is only a theoretical solution. Indeed, the evolutionary species is a hypothesis, being a part of a hypothesized phylogenetic tree. The biological species, on the other hand, is distinguished on the basis of direct observation or it can be established experimentally. This is, however, not the place to discuss theoretical matters thoroughly. Here we will confine ourselves to drawing attention to this interesting situation.
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REFERENCES


