Man As an Agent of Crustacean passive dispersal via useful plants-exemplified by Ostracoda *Ospiti Esteri* of the Italian ricefields ecosystem-and implications arising therefrom

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Abstract

The eggs of many crustaceans are minute and resistant to desiccation. These properties favour their accidental dispersal and parthenogenesis ensures survival in the newly occupied niches. Agencies by which such dispersal is achieved have been long ensconced in the literature. The role of man as an agent of crustacean dispersal via the spread of useful plants, however, has been relatively neglected hitherto but the example provided by ostracode ospiti esteri of the Italian ricefields ecosystem indicates that this neglect is unwarranted. Italian historical and archaeobotanical records concerning the introductions of numerous other useful plants make it obvious that the dispersal potential of this agency cannot be restricted to rice only. When modern Ostracoda assemblages from Europe are compared against fossil ones, their dissimilarity suggests a high proportion of introduced species in the modern biota. The implications of this are discussed.

Students of crustacean biogeography must come to terms with several aspects of crustacean physiology that can affect distribution patterns. One such aspect is the ability of numerous crustaceans inhabiting terrestrial aquatic ecosystems to reproduce parthenogenetically. The widespread dispersal of many taxa, even in tercontinentally, has been linked frequently to this phenomenon which is known as geographic parthenogenesis.

We stress two particular facets of geographic parthenogenesis: firstly, that parthenogenetic populations tend to form the dispersal fringe of the taxa concerned; secondly, that where amphigonic populations are also known for the taxa under study they tend to be confined to the zoogeographic regions where these taxa are native (McKenzie, 1971a). Some possible exceptions will be discussed later, but these serve only to accentuate rather than invalidate our ideas.

Another germane aspect of crustacean physiology is the ability of many taxa to produce desiccation-resistant eggs; and linked to this is the fact that the eggs of most crustaceans that inhabit terrestrial aquatic ecosystems are very small — for Ostracoda they rarely exceed 50-μm diameter. The combination of resistance to desiccation and minute size makes it unsurprising that passive dispersal is the rule for these Crustacea, as confirmed by a vast literature that is recycled regularly by reviewers.

Our purpose in this paper is to stress the hitherto little emphasised role of man as an indirect agent of crustacean passive dispersal via the spread of useful plants. Our exemplars are Ostracoda of the ricefields ecosystem, specifically some species introduced into the major Italian rice-growing region of Lombardy-Padana (Fig. 1). We also cite records (historical as well as archaeoethnobotanical) of the introduction into Italy of rice and many other useful plants via which desiccation-resistant ostracode eggs might have been incidentally dispersed. Our discussion of this more general hypothesis will conclude with reference to comparisons between fossil and modern European ostracode assemblages.

Ostracoda Of The Italian Ricefields Ecosystem

Most ostracodes appear in Italian ricefields only when the aquatic cycle becomes more or less permanent. That is, they characterise the intermediate and climactic heleoplankton communities, rather than the pioneer community which is dominated by Cladocera with associated cyclopoid copepods, chironomids, and occasional anostracans, conchostracans, and notostracans (Rossi *et al,* 1974).

In a useful synthesis, Ghetti and McKenzie (1981) recorded about 65 ostracode species from the Italian ricefields, listing their occurrence by regions. Specimens of most of these taxa are retained in collections at the Istituto di Ecologia, Parma, where almost all research into Italian ricefields Ostracoda has been carried out, and other collections are held at the Istituto di Idrobiologia "Dott. Marco De Marchi," Pallanza. Recently, the senior author (K.G.M.) was able to review both collections. Table 1 is an updated species list based on the results of these reviews. It includes several species which remain indeterminate because the collections contain only juvenile stages poorly preserved on dissection slides. Further, one taxon *(Heterocypris* sp. 1) could not be determined to species due to a lack of comparative type material at Parma of this very large genus when the check was undertaken. There are several variations in the updated list from that which can be abstracted from Ghetti and McKenzie (1981). In particular, *Physocypria armata* (G.W. Mueller, 1898) is removed altogether from the Italian fauna (K.G.M. reassigned the dissection slide to *Heterocypris).* Because our data relate only to 12 Italian ricefields it seems unlikely that Table 1 is a complete list. Other ricefields are now being sampled regularly as part of the Istituto di Ecologia program and these collections may well add several taxa to the existing Italian ricefields ostracode fauna. Nevertheless, the corrected list still amounts to over 50 species.

Among the ostracodes regularly sampled from Italian ricefields are several non-European introduced species which we call *ospiti esteri.* We define *ospiti esteri* (Italian for "foreign guests") as species known to be native elsewhere, i.e., foreign in origin, but also occurring as parthenogenetic taxa in the Italian ricefields. Our concept may well prove to have more general application for explaining parthenogenetic dispersal patterns, but we prefer for the moment to restrict it to an ecosystem with which we are familiar and for which our data extend over a considerable number of years. A list of Italian *ospiti esteri* is provided in Table 2. No males of these *ospiti esteri* have yet been found in Italy. They may be regarded, therefore, as characteristic examplars of geographic parthenogenesis.

Geographic Parthenogenesis

Geographic parthenogenesis is usually understood as the tendency for some taxa to occur as parthenogenetic populations in one part of their range but as amphigonic populations elsewhere. In attempting to explain this phenomenon, Tetart (1975) reviewed the observations of numerous authors and experimented with a number of ecological factors concluding that the most important factor might well be temperature. He noted that for many species parthenogenetic populations are found in the colder parts of Europe, whereas in southern Europe and North Africa syngamic populations are common.

Another ecological factor of importance granted a sufficient ambient temperature is the nature of the habitat, particularly whether it is intermittent or permanent. The ricefields, of course, although they have a high ambient temperature, are an intermittently aquatic habitat, and this may well contribute to the maintenance of parthenogenesis in ricefield populations of the *ospiti esteri.* This factor is also effective in the areas of origin. Thus, the senior author has collected several parthenogenetic populations of *Chlamydotheca,* the endemic South and Central American cypridacean genus, in adventitious habitats, such as roadside ditches in Argentina, whereas in permanent aquatic environments males usually occur. Similarly, in Australia, *Bennelongia* (another cypridacean) occurs as parthenogenetic populations in impermanent habitats, including small ponds and roadside ditches, while the syngamic populations are found in permanent lakes (De Deckker, 1981). De Deckker (personal communication, November 1981) confirmed that this is also the case with the Australian endemic genus *Mytilocypris.* But such parthenogenesis is

really a variety of sympatry. While the parthenogenetic and amphigonic populations certainly occupy distinct ecological niches, the chances of dispersal between the two niches are relatively high. Presumably, a stress factor operates in the intermittent environments, inducing species to switch to a parthenogenetic mode.
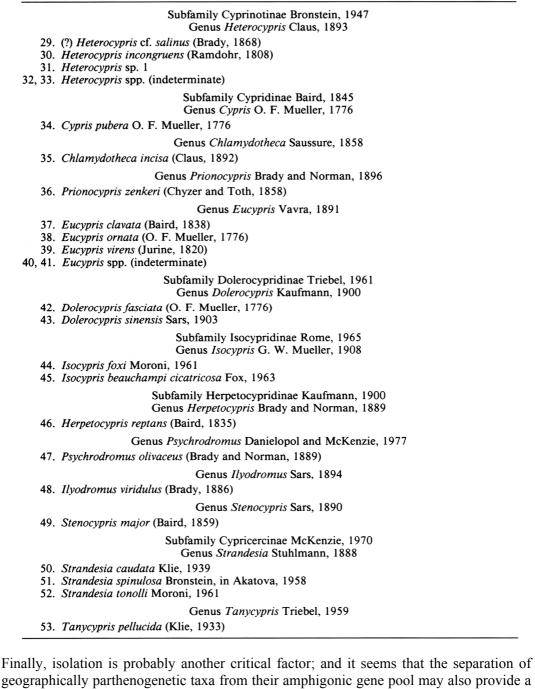

Fig. 1. Locations of the 12 Italian ricefields studied for this paper. 1 = Barze (Vespolate, Novara); 2 = Olza (Casalpusterlengo, Milano); 3 = Maina (Mede, Pavia); 4 = Zanella (Mozzecane, Verona); 5 = Pegoraro (Camisano, Vicenza); 6 = Cantarella (Bagnolo di Lonigo, Vicenza); 7 = Ca'Nuova (S. Antonio, Mantova); 8 = Guagnino (Comacchio, Ferrara); 9 = Cortenuova (Novellara, Reggio Emilia); 10 = La Vecchia (Gualtieri, Reggio Emilia); 11 = Merse (Murlo, Siena); 12 = Siviero (Simaxis, Oristano). Currently under intensive study is La Bigliana (Gualtieri, Reggio Emilia), near 10.

Table 1. Revised list of Italian ricefields Ostracoda, based on collections at the Istituto di Ecologia, Parma, and at the Istituto di Idrobiologia, Pallanza.

Superfamily Cytheracea Baird, 1850
Family Cytheridae Baird, 1850
Genus *Limnocythere* Brady, 1867

1. *Limnocythere inopinata* (Baird, 1843)
2. *Limnocythere* cf. *stationis* Vavra, 1901

Superfamily Cypridacea Baird, 1845
Family Ilyocyprididae Kaufmann, 1900
Genus *Ilyocypris* Brady and Norman, 1889

3. *Ilyocypris australiensis* Sars, 1890
4. *Ilyocypris biplicata* (Koch, 1838)
5. *Ilyocypris decipiens* Masi, 1906, *veneta* Moroni, 1961
6. *Ilyocypris gibba* Ramdohr, 1808

Genus *Ilyocyprella* Sars, 1925

7. *Ilyocyprella inermis* (Kaufmann, 1900)

Family Candonidae Kaufmann, 1900
Genus *Candona* (*Candona*) Baird, 1845

8. *Candona* (*Candona*) *candida* (O. F. Mueller, 1785)
9. *Candona* (*Candona*) *neglecta* Sars, 1887

Genus *Candona* (*Fabaeformiscandona*) Krstic, 1972

10. *Candona* (*Fabaeformiscandona*) *fabaeformis* Fischer, 1854
11. *Candona* (*Fabaeformiscandona*) *fragilis* Hartwig, 1901

Genus *Candona* sensu lato

12. *Candona* sp. (indeterminate juveniles)

Genus *Paracandona* Hartwig, 1899

13. *Paracandona euplectella* (Brady and Norman, 1889)

Family Notodromadidae Kaufmann, 1900
Genus *Notodromas* Lilljeborg, 1853

14. *Notodromas persica* Gurney, 1920 *dalmatina* Petkovski, 1959

Family Cypridopsidae Kaufmann, 1900
Genus *Cypridopsis* Brady, 1868

15. *Cypridopsis elongata* Kaufmann, 1900
16. *Cypridopsis hartwigi* G. W. Mueller, 1900
17. *Cypridopsis helvetica* Kaufmann, 1900
18. *Cypridopsis obesa* Brady and Robertson, 1869
19. *Cypridopsis parva* G. W. Mueller, 1900
20. *Cypridopsis vidua* (O. F. Mueller, 1776)

Genus *Potamocypris* Brady, 1870

21. *Potamocypris arcuata* (Sars, 1903)
22. *Potamocypris fulva* (Brady, 1868)
23. *Potamocypris smaragdina* (Vavra, 1891)
24. *Potamocypris villosa* (Jurine, 1820)

Family Cyprididae Baird, 1845
Subfamily Cyprettinae Hartmann, 1963
Genus *Cypretta* Vavra, 1895

25. *Cypretta* cf. *dubia* (Daday, 1901)
26. *Cypretta* cf. *globulus* (Sars, 1890)
27. *Cypretta seurati* Gauthier, 1929
28. *Cypretta turgida* (Sars, 1895)

Table 1. Continued.

Subfamily Cyprinotinae Bronstein, 1947
Genus *Heterocypris* Claus, 1893

29. (?) *Heterocypris* cf. *salinus* (Brady, 1868)
30. *Heterocypris incongruens* (Ramdohr, 1808)
31. *Heterocypris* sp. 1
32, 33. *Heterocypris* spp. (indeterminate)

Subfamily Cypridinae Baird, 1845
Genus *Cypris* O. F. Mueller, 1776

34. *Cypris pubera* O. F. Mueller, 1776

Genus *Chlamydotheca* Saussure, 1858

35. *Chlamydotheca incisa* (Claus, 1892)

Genus *Prionocypris* Brady and Norman, 1896

36. *Prionocypris zenkeri* (Chyzer and Toth, 1858)

Genus *Eucypris* Vavra, 1891

37. *Eucypris clavata* (Baird, 1838)
38. *Eucypris ornata* (O. F. Mueller, 1776)
39. *Eucypris virens* (Jurine, 1820)
40, 41. *Eucypris* spp. (indeterminate)

Subfamily Dolerocypridinae Triebel, 1961
Genus *Dolerocypris* Kaufmann, 1900

42. *Dolerocypris fasciata* (O. F. Mueller, 1776)
43. *Dolerocypris sinensis* Sars, 1903

Subfamily Isocypridinae Rome, 1965
Genus *Isocypris* G. W. Mueller, 1908

44. *Isocypris foxi* Moroni, 1961
45. *Isocypris beauchampi cicatricosa* Fox, 1963

Subfamily Herpetocypridinae Kaufmann, 1900
Genus *Herpetocypris* Brady and Norman, 1889

46. *Herpetocypris reptans* (Baird, 1835)

Genus *Psychrodromus* Danielopol and McKenzie, 1977

47. *Psychrodromus olivaceus* (Brady and Norman, 1889)

Genus *Ilyodromus* Sars, 1894

48. *Ilyodromus viridulus* (Brady, 1886)

Genus *Stenocypris* Sars, 1890

49. *Stenocypris major* (Baird, 1859)

Subfamily Cypricercinae McKenzie, 1970
Genus *Strandesia* Stuhlmann, 1888

50. *Strandesia caudata* Klie, 1939
51. *Strandesia spinulosa* Bronstein, in Akatova, 1958
52. *Strandesia tonolli* Moroni, 1961

Genus *Tanycypris* Triebel, 1959

53. *Tanycypris pellucida* (Klie, 1933)

Finally, isolation is probably another critical factor; and it seems that the separation of geographically parthenogenetic taxa from their amphigonic gene pool may also provide a trigger for diversification, effectively refuting the usual argument that parthenogenesis is an evolutionary dead end (see also Lynch and Gabriel, 1983). For example, several *Isocypris* species have been described from Europe, all of them being parthenogenetic, including a couple of ricefields species (Table 2). In its area of origin, which is South Africa, however, *Isocypris* commonly occurs as bisexual populations but is relatively poor in species. All the ricefields ostracode *ospiti esteri* exhibit parthenogenesis by thelytoky (female diploid parthenogenesis). The thelytoky may be induced ecologically in otherwise sexually reproducing taxa or may be inferred to be complete for those species for which males are as yet entirely unknown. Tetart (1975) noted that, cytologically, the difference between sexual and thelytokous females lies in the maturation of the ovocytes. After a cytological study of nearly 30 species in the families Darwinulidae, Cytheridae, and Cyprididae, Tetart (1978) concluded that many species displayed modified caryotypes and that the modifications appeared to be relatively recent (in an evolutionary sense) and were much more common in parthenogenetic species.

Table 2. Ostracode *ospiti esteri* in the Italian ricefields ecosystem, their regions of origin and some plausibly associated useful plants.

Ostracode species	Region of origin	Some possible dispersal associates
Chlamydotheca incisa	South America	tobacco, tomato, sunflower
Dolerocypris sinensis	China, Southeast Asia	rice, mulberry, peach, hemp
Tanycypris pellucida	Southeast Asia	rice, spices
Strandesia (3 spp.)	Africa, Asia	rice, hemp, saffron
Stenocypris major	India, Ceylon	rice, hemp, spices, cotton
Ilyodromus viridulus	Australia	rice
Isocypris (2 spp.)	Africa	wheat, saffron, cotton
Notodromas persica	Central Asia	rice, mulberry, peach, hemp
Cypretta (3 spp.)	mainly Asia	rice, hemp, cotton, spices

Taking a different approach, masculinisation in many crustaceans is developed physiologically by androgenic glands (Charniaux-Cotton *et al.,* 1966) with the active component likely being a proteinaceous androgenic gland hormone (Katakura and Hasegawa, 1983). Evidently, the ecological factors we have discussed above (temperature, intermittently aquatic habitat, isolation) militate against production of this hormone, at least in ecologically thelytokous females of the *ospiti esteri*— assuming that lower crustaceans such as ostracodes also possess androgenic glands, similar to those of most malacostracan orders, or their functional equivalents.

Whatever the precise nature of the inhibiting effects of ecological factors upon parthenogenetic ricefields ostracodes, it is vital to make the point that they apparently have no deleterious influence on the production of desiccation-resistant eggs by these taxa. In this context, the observation of Ghetti (1973a), that ostracode populations in ricefields were dominated by juveniles no matter what the crop stage was, strongly suggests that clutches of resistive eggs buried in the substrate mud hatch throughout the crop cycle. Further, when dried ricefields mud is cultured in an aquarium, juvenile ostracodes soon appear and develop as parthenogenetic females (Fox, 1965; Okubo, 1972, 1973a, b, 1974a, b, 1975).

Possible Exceptions to the McKenzie (1971a) Hypothesis

The Database

Before discussing exceptions to the McKenzie (1971a) hypothesis (outlined briefly above) as it affects ostracode *ospiti esteri* of the Italian ricefields ecosystem, it seems useful to indicate the size of the available database. Unquestionably, most work has been done on the Italian ricefields (Manfredi, 1932; Fox, 1965; Moroni, 1967; Ghetti, 1973a), but numerous ricefields in other areas have also been studied for their ostracode faunas. The following citations should be regarded as conservative: Burundi (Ghetti, 1970); the Camargue, France (Schachter and Conat, 1952; Steger, 1972); Yugoslavia (Papovska-Stankovic, 1960; Petkovski, 1964); Turkey (Ghetti, 1973b); Persia (Ghetti, 1973b; Yassini, 1976); southern Russia (Bronstein, 1947; Muhamediev, 1960); India (Singh, 1971; Victor and Fernando, 1978); Sri Lanka (Neale, 1977); southeast Asia (Malaysia, Indonesia, the Philippines) (Victor and Fernando, 1980); Japan (Okubo, 1972; and subsequently). Additionally, the senior author has sampled ricefields near Nanjing, China (in July 1983) and is committed to a study of Australian ricefields Ostracoda (correspondence with D.S. Mitchell, January 1985). Thus, with respect to the worldwide distribution of rice cultivation, the main gaps in knowledge concerning the associated Ostracoda relate to Madagascar, East and West Africa, South America, and the Gulf Coast region of the United States (Moormann and van Breeman, 1978, fig. 2).

Possible Exceptional Cases

All records of ricefields *ospiti esteri,* whether of individuals or populations, are exclusively parthenogenetic. Nevertheless, some data suggest that perhaps five families/

subfamilies of ostracodes may be exceptions to the McKenzie (1971a) hypothesis. These taxa are Cyprinotinae, Candoninae, Cypridopsidae, Cypricercinae, and Ilyocyprididae. Careful consideration of the evidence, however, has eliminated all of them.

We are aware of only two records of ostracode males from ricefields. Firstly, a male of *Candona (Fabaeformiscandona) fabaeformis* Fischer, 1854, was collected in the Cortenuova ricefield, Emilia-Romagna (Fig. 1), on 16 June 1962; and secondly, Okubo (1974a) collected males of *Cyprinotus uenoi* Brehm, 1936, from ricefields in Japan. However, both taxa are characteristic species of the same zoogeographic regions as the ricefields in which they were collected. Thus, they are not *ospiti esteri* as defined by us.

The other possibly exceptional families/subfamilies include genera which are known to be amphigonic either in more than one zoogeographic region or in collections made near ricefields. Examples of the first category are *Plesiocypridopsis* and *Ilyocypris;* and the second category includes *Plesiocypridopsis* (again) and *Strandesia* (McKenzie, 1971b; Hartmann, 1964; Victor and Michael, 1975; Rome, 1965; Neale, 1977). No males of the genera belonging to these families and subfamilies have ever been recorded from ricefields anywhere to our knowledge.

Passive Dispersal of Ostracoda

The passive dispersal of Ostracoda was reviewed by McKenzie and Hussainy (1968) as part of an experimental study that demonstrated the low vagility of taxa that lacked desiccation-resistant eggs. Subsequently, McKenzie (1971a) correlated passive dispersal with parthenogenesis, pointing out that numerous introduced species having desiccation-resistant eggs were known to reproduce only by the parthenogenetic mode in the niches to which they had accidentally dispersed. Other workers have either reemphasised the role of some previously proposed agents of ostracode passive dispersal, such as birds (De Deckker, 1977), or have discussed new agencies.

Passive dispersals via such agencies as torpidity, fish, and high winds (Delorme and Donald, 1969; Kornicker and Sohn, 1971; Sohn and Kornicker, 1979) seem to have little relevance for the Italian ricefields ecosystem. For torpid forms to be dispersed, the mud in which they are resting-over has to be transported from the ricefield by some other agent such as strong wind (when the ricefield has dried out), or attached to birds' legs and feathers, or into irrigation ditches (when the ricefield is "flushed" to clear out algal blooms, etc.), or by man working in the ricefield. Fish are not cultured in Italian ricefields, as they are, for example, in Indonesia and the Philippines. And it seems most unlikely that high altitude winds could carry any ostracodes (or their eggs) intercontinentally and then deposit them preferentially in Lombardy-Padana (some introduced species are recorded in Europe only from the Italian ricefields). However, ostracodes might well be drift-borne into ricefields via irrigation channels during the aquatic phases of the crop cycle. Possibly, the extremely rare records of males from Italian ricefields can be ascribed to this factor. In this context, we mention again that the Istituto di Ecologia collections include only one such male of *Candona (Fabaeformiscandona) fabaeformis* Fischer, 1854, taken in the Cortenuova ricefield, Emilia-Romagna, on 16 June 1962; and this taxon is not a "foreign guest."

A number of experiments carried out by Proctor (1964) and Proctor and Malone (1965) in the southern United States support the idea that migrating waterfowl can swallow ostracode eggs while feeding at one body of water and defecate them into another some distance away without inhibiting their viability, thanks to the resistant double-wall structure of the eggs. For this hypothesis to be developed rigorously in the context of the Italian ricefields ecosystem the migrating patterns of waterfowl which feed in the ricefields need to be known and should correlate positively with the regions of origin of non-European introduced ostracode species. Further, since vast distances are involved (one introduced Italian ricefields ostracode originates in South America, others in South Africa and Australia) intermediate records of the passively dispersed taxa, between their regions of origin and Italy, are necessary. Similarly, while Loffler and Leibetseder (1966) demonstrated that ostracode eggs can survive in a bird's crop for periods ranging from 30

min to a few hours, thus indicating a possibility of successful intercontinental transport, there has been no definitive test of the thesis, for example, using banded migratory birds. Summing up, the experimental work hitherto (1964) clearly does *not* prove definitively that either ostracodes or their desiccation-resistant eggs can be ingested and ferried *intercontinentally* by birds and still survive. It remains plausible that waders and littoral-feeding birds can pick up mud containing live Ostracoda and/or their desiccation-resistant eggs on their legs and feathers and transport them, but this suggestion also has been inadequately tested.

Meanwhile, the association between introduced Ostracoda and useful (including ornamental) plants had been noted by Triebel (1959) who described females of *Dolerocypris sinensis* Sars, 1903, originally described from China, from a collection made in the botanical garden at Frankfurt-am-Main, Germany. Fox (1965) was the first to suggest that the *ospiti esteri* had been introduced with trial strains of rice seed, an idea which was endorsed by Moroni (1967) and McKenzie (1971a). Subsequently, Neale (1977) adopted rice seed exchanges in the historical past between Indonesia and Sri Lanka to account for some elements of the ostracode fauna in Sri Lankan ricefields. Victor and Fernando (1980) reevaluated Neale's data and concluded that his hypothesis was unnecessary to explain the particular distributions he discussed, which they found to be contiguous. These authors concluded in favour of a variety of transporting agencies including irrigation channels, winds, and birds (nomadic or migratory) as well as rice seed exchanges (Victor and Fernando, 1980).

Rice and Other Useful Plant Introductions into Lombardy-Padana and Italy Generally

There is no doubt that, in the context of the passive dispersal of *ospiti esteri* into the Italian ricefields ecosystem, the useful plant most likely to be associated is rice itself, through seed exchanges. However, by focusing solely upon rice, the several authors quoted in the preceding section ignored a more general hypothesis by which numerous other useful plants could have been responsible for the same effect at any time in the past, from prehistorical ages (for which the evidence is adduced via archaeobotanical materials), through historical time (when ethno-botanical records can be quoted), to the recent past. The advantages of using Italy as an exemplar region in the context of this general hypothesis are the abundance of such introductions and the comparative excellence of Italian historical records, at least from Roman times to the present.

Rice

Rice *(Oryza sativa* L.) was domesticated in tropical and subtropical southeastern Asia where its cultivation is known to be extremely ancient (Moormann and van Breeman, 1978). It occurs at Khok Phanom Di, Thailand, in archaeological deposits dated at around 7,000 B.P. (C.F. Higham, personal communication, April 1985) and also in Chinese remains of the Yangshao Culture which are similar in age (Bai, 1982). From its centre of origin the crop spread worldwide and is now man's most important staple. Its introduction into Persia, Asia Minor, and Macedonia followed upon Alexander's expedition and it was established in these regions by the third century B.C. (Huke, 1976). From the near East, the Romans carried rice across Europe. Grains of rice have been identified at Neuss/Rhineland in Roman remains from the first century A.D. (Knorzer, 1970). But it is not yet known whether such remains represent an imported luxury item (Knorzer, 1966) or a Mediterranean crop (H. Kroll, personal communication, January 1985). Rice was established in Africa by traders and emigrants from India to Madagascar and East Africa, by the Ptolemys in Egypt, and by the Arabs, probably, in West and North Africa. The Moors took it to Spain in the ninth century A.D. from where it reached the Americas in the fifteenth century (the Caribbean, Mexico, and Brazil). Finally, the crop was introduced into Australia from Indonesia towards the end of the last century (Huke, 1976).

Rice is a semiaquatic plant; thus, ricefields may be thought of as periodically aquatic islands surrounded by land. The dispersal history referred to briefly above makes it clear that the Italian ricefields are also islands in the historical sense, because rice is not native to Italy.

In a monograph on rice cultivation in Italy, Chiappelli (1930) listed some 39 varieties of *Oryza sativa* together with the years when they were introduced and countries of origin when known. Most of these varieties were Asiatic in origin (China, Indonesia, Japan) with others coming from the United States, Spain, and Madagascar. A few varieties were cited simply as "old." They included Ostiglia and Chinese Ostiglia, the varietal name coming from an important river port on the Po, between Mantova and Ferrara in the extensive Lombardy plain. More recently, some Australian rice strains have been tested.

Apart from a brief, unsuccessful attempt to establish risiculture near Pisa in 1468, the Lombardy plain has always been the main producing region in Italy for this crop. The earliest historical reference is contained in a letter dated 1475 from the Duke of Milan, Galeazzo Maria Sforza, requesting 12 sacks of seed rice from Ercole I, Duke of Ferrara, from which it can be assumed that Ferrara was already an important rice district; indeed it is likely that by this time risiculture was widespread along the Adriatic coast from Ravenna to Udine (Zucchini, 1967). However, rice was not grown near Ferrara by 1287, since it is not among the crops listed in the Statuto Ferrariae of that date (Zucchini, 1967). Probably, it did not assume importance for the Ferrara dukedom until the first half of the fifteenth century when the dukes began a series of bonifactions, clearing of forests and drainage of swamps into the Po and Adige by a network of canals, thus creating vast new areas of arable land in order to support a rapidly increasing population.

These bonifactions had been initiated by the great abbeys in the early Middle Ages, and were continued in the later Middle Ages by the communal councils which governed many towns in the period preceding the rise of the great Renaissance dukedoms. We know from the abbatial records of foundations such as Pomposa that risiculture was not established locally much earlier than it began near Ferrara, the principal crops until then being vines, olives, and flax, and much land being developed as pasture (Zucchini, 1967: 40-46).

Other Useful Plants

Lombardy and Padana are not only the main rice-growing districts of Italy; they are or were very important also for numerous other crops, including some with a considerable antiquity of introduction into Italy. For example, wheat *(Trit-icum)* was grown in Lombardy-Padana about 6,000 years ago (Forni, 1979), but arrived in Italy much earlier, at least 7, 110 B.P. (Follieri, 1982). Barley, bitter vetch, bean, and lentil were all cultivated in Greece prior to 7,000 B.P. (Kroll, 1984) and introduced into Italy penecontemporaneously (Follieri, 1982). The centre of origin for this early agriculture was the near East (Lawton and Wilke, 1979).

Apart from such staples, the prehistoric Italian agrarian economy soon became more diversified. Thus, flax *(Linum)* is known from about 4,800 B.P. (Forni, 1979). Furthermore, hemp *(Cannabis)* which was valued by early man as providing strong cordage was established in Italy by the first century B.C. (G. Rivoira, personal communication, June 1982). Hemp would have been grown in northern Italy from the early part of the first century A.D., when Augustus established an Adriatic fleet based at Classis, near Ravenna. It was a major crop around Ferrara by the thirteenth century, being cited in the Statuto Ferrariae (Zucchini, 1967), and in 1939 60% of the Italian production of hemp was shared between Ferrara and Bologna (Coggi, 1939). Further, nearly 50% of the fruit exported by Italy comes from this region, especially apples, pears, peaches, and cherries (Avellini *et al.*, 1980), and in many districts orchards have been established since the Middle Ages. Of these fruits, the peach *(Prunus persica)* which grows readily from its stones orginated in China where it is recorded from about 1,000 B.C. and was introduced into Italy by the first century A.D., since it is illustrated on the walls of Pompeii (De Candolle, 1886/1959). Vines *(Vitis)* were first cultivated in Lornbardy-Padana much

earlier, around 7,000 B.P. (Forni, 1979: 42), and figs *(Ficus)* have been recorded from Lombardy-Padana since the Bronze Age (about 3,500 B.P.) (Forni, 1979).

The cultivation of some other exotic plants is linked with the growing significance of northern Italy as a centre for textile production from about the thirteenth century. Important towns in the early period of this development were Pisa, Pavia, and Lucca, but it soon became widespread. The main crops were those which provided tinting materials—guado (black), robbia (madder), scotano (fustian), zafferano (saffron), etc. — and also white mulberry *(Morus alba),* which was widely grown around Bologna, for example, by the fourteenth century (Borlandi, 1950; Bignardi, 1978). Cultivation of mulberry, the seeds of which germinate readily, is linked with sericulture. This industry originated in China where mulberry is recorded on Shang Dynasty (sixteenth-eleventh century B.C.) oracle bones (Bai, 1982: 72).

Also grown in northern Italy around the late Middle Ages (eleventh-thirteenth centuries A.D.) were Asian spices as anice (aniseed), comino (cumin), and corian-doli (coriander) (Bignardi, 1978). The last-named is first recorded from Italy much earlier in deposits dated fourth century A.D. sampled near the Coliseum at Rome (Follieri, 1975), but likely was imported then. These cultivations began as a result of the great expansion in commerce arising from contacts with the Levant which became more frequent following the Crusades.

With the discovery of the Americas, numerous other crops were introduced from there into north Italy, notably tobacco, tomato, potato, and sunflower, in the sixteenth and seventeenth centuries (Zucchini, 1967: 177-178).

Of course, it was not only Lombardy that was so affected. For example, Frederick II of Naples introduced cotton and sugar cane around Naples about 1230 on his return from the second Crusade (Gleijeses, 1977).

Finally, the development of botanical gardens from the early seventeenth century onwards was another avenue by which exotic plants and animals, including Ostracoda, could have reached Italy. The first such garden was established at Genoa.

Relevance for Ostracode Dispersal

With such a plethora of crops introduced from every quarter of the globe it is scarcely remarkable that *ospiti esteri* are often found in the Italian ricefields. The minute desiccation-resistant eggs of cypridacean ostracodes might easily have been imported into Italy with seeds of exotic cereals and useful plants, in soil packed around cuttings, in dust brought in with trade goods, and by travelers or migrating peoples.

Table 2 lists some undoubted ostracode *ospiti esteri* of Lombardy-Padana, their regions of origin, and some plants with which their desiccation-resistant eggs might have become dispersed in the ways noted. Once introduced they could easily move into the aquatic islands which constitute the Italian ricefields ecosystem and their eggs would require only an aquatic phase to hatch.

While most of these *ospiti esteri* are tropical and subtropical species their survival is not surprising because even at the northern Italian latitudes ambient temperatures of around 25-35°C are typical in the Lombardy ricefields, especially during summer (June-August). Thus, temperature, which is linked elsewhere with parthenogenetic reproduction (Tetart, 1974, 1975), is not a determinative factor for Italian ricefields ecosystems. It seems, rather, that it is the aperiodic astatic character of ricefields as well as the isolation of Italy from their Asian, Australian, African, and South American centres of origin that accounts best for the exclusively parthenogenetic populations of the *ospiti esteri* recorded in Table 2.

Comparison with European Fossil Assemblages

Interpretations of ostracode biogeography are constrained by the fact that any hypotheses regarding modern distributions are testable by reference to a fossil record which is considerably more diverse and abundant than that of any other group of crustaceans. Our

hypothesis, that man is mainly responsible for the introduction of ostracode *ospiti esteri* into northern Italy via his cultivation and dispersal of useful plants, notably rice, is certainly susceptible to this test. If we can demonstrate that *ospiti esteri* do not occur in Tertiary and Quaternary (Pleistocene-early Holocene) European fossil assemblages— when we can assume confidently that different dispersal agencies such as winds and birds were operative but rice and other useful plants were not yet cultivated—then our hypothesis passes the test.

There is only one major reference to Italian Quaternary fresh-water Ostracoda (Devoto, 1965) and the several short papers on Italian Late Tertiary fresh-water faunas do not include any of the *ospiti esteri* listed in Table 2. Devoto (1965) listed 35 species from the lacustrine Pleistocene of the Liri Valley, mid-Apennines, of which one is identified as *Ilyodromus olivaceus.* However, Danielopol and McKenzie (1977) showed that this species and related taxa had no close relationship to *Ilyodromus* sensu stricto and established a new Holarctic genus, *Psy-chrodromus,* for the group. The Devoto list also contains *Cypricercus reticulatus* (Zaddach, 1844); and *Cypricercus* is often confused with *Strandesia,* one of the "foreign guest" taxa (Table 2). Again, McKenzie (1982) and Broodbakker (1983) have indicated that there is a generic misnomer problem and that Holarctic species in this group belong in a new genus *Bradleystrandesia* Broodbakker, 1983.

Although the Italian references are limited there is a vast literature on the Ostracoda of the Tertiary Paratethyan basins to the north which range from southern USSR all the way across to France and have been closely studied especially in the USSR and the Balkans because of their application in petroleum exploration. These are the world's best known fresh-water or brackish Late Tertiary ostracode faunas. Additionally, the regional Pleistocene deposits, particularly of Germany and Bohemia, have been carefully studied. Thus, the database for comparison is large and it is unlikely that the *ospiti esteri* (all distinctive genera) would have been missed if they were present.

Paratethyan faunas are equally distinctive. They are characterised also by a high degree of endemism from basin to basin which is appropriate to the geological record of a gradually shrinking Paratethys becoming a series of discontinuous basins which individually gradually disappeared during the Pliocene and post-Pliocene. The major papers are: southern USSR (Mandelshtam *et al.*, 1962; Man-delshtam and Schneider, 1963; Sheidaeya-Kulieva, 1966); Rumania (Hanganu and Papaianopol, 1977); Bulgaria (Stancheva, 1964, 1965, 1971, 1972); Yugoslavia (Sokac, 1972; Krstic, 1973); Hungary (Zalanyi, 1944); Czechoslovakia (Pokorny, 1952); Germany (Malz and Moayedpour, 1973); France (Carbonnel, 1969). Many zones and facies are brackish (some marine) but fresh-water units occur in all basins. There are no records of any of the *ospiti esteri* genera listed in Table 2 with the exceptions of *Dolerocypris* and *Ilyodromus,* both of them listed by the authors concerned as questionable generic determinations (Kazmina, 1975; Krstic, 1971). The shape of Kazmina's taxon is quite unlike *Dolerocypris* which is a genus of elongate form; and the two species referred by Krstic (1971) to *Ilyodromus* belong likely to *Psychrodromus.*

There are several records of *ospiti esteri* genera from deposits other than the Miocene (Kempf, 1980). Most of them, however, relate to taxa from the Mesozoic and cannot be sustained as representing the genera in which they have been placed, namely *Cypretta, Dolerocypris,* and *Stenocypris* (Grekoff, 1957, 1960). Of the others, *Strandesia spinosa* Stchepinsky, 1960, described from the Oligocene of Alsace, is not a *Strandesia* (based on the illustration in Carbonnel and Ritzkowski [1969] it is a new genus); and species assigned to *Stenocypris* by Zalanyi (1929) and Grekoff (1958) fare little better. *Stenocypris venusta* Zalanyi, 1929, has been placed in the candonid subgenus *Zalanyiella* (Krstic, 1972), which is unrelated to *Stenocypris. Stenocypris* (?) *bunzaensis* Grekoff, 1958, lacks the diagnostic radial septa of *Stenocypris* sensu stricto.

There remain the post-Pliocene records. The major papers include: a large series by Diebel and Pietrzeniuk (1969, 1978a, b, 1984) for Germany; Robinson (1978) and De Deckker (1979) for the United Kingdom; Kheil (1965) and Absolon (1973a, 1974) for Bohemia and central Europe. The only *ospiti esteri* genera referred to in these and other

shorter papers are *Dolerocypris* and *Ilyodromus*. Records of the latter, such as Absolon (1973b) and Kempf and Scharf (1980) belong properly to *Psychrodromus;* while *Dolerocypris* is always recorded as *D. fasciata* (O.F. Mueller, 1776), the ubiquitous Holarctic taxon, rather than the distinctive oriental "foreign guest" species *D. sinensis* (Diebel and Pietrzeniuk, 1984).

In summary, the fossil record yields a positive result for our hypothesis, since there are no verifiable records from the Cainozoic of Europe of any of the *ospiti esteri* taxa (genera and species) listed in Table 2. We are absolutely confident that none could exist for the Tertiary and most of the Quaternary and assert that any future subfossil Holocene records will most probably be associated with human settlements.

Conclusions

Italian ricefields Ostracoda are both diverse and common, being associated mostly with late stages in the crop cycle. They reproduce parthenogenetically and include numerous (about one-fourth of the total known fauna) "foreign guest" species which we term *ospiti esteri*. We consider that these have been transported into Italy by man via rice seed exchanges or with seeds and cuttings of other useful plants. Historical, ethnobotanical, and archaeoethnobotanical evidence all indicates that the introductions have occurred within the past 10,000 years (the Holocene). Fossil evidence for the Tertiary and Quaternary confirms that no *ospiti esteri* genera or species occur in the pre-Holocene faunas of Europe. Several useful conclusions can be drawn.

Firstly, the observation that some taxa which are amphigonic in their regions of origin occur in Italian ricefields only as parthenogenetic populations provides a test to determine the *ospiti esteri* in any assemblage. The native species of any region should be recorded as amphigonic populations, at least in permanent aquatic habitats, within that region. Exceptions to this generalisation would be taxa which as far as known are wholly parthenogenetic (some *Cypridopsis* species, for example); or which by reason of their long geological history have established amphigonic populations across several zoogeographic regions (such as Ilyocypri-didae, Cyprinotinae, *Plesiocypridopsis).*

Secondly, because ricefields are impermanent aperiodic aquatic environments with particular climatic and plant associations and a brief history (at most around 8,000 years) their faunas should not be extrapolated to interpret the palaeocology even of impermanent fossil environments unless the *ospiti esteri* are removed from the modern biotas. Even so, comparisons would be difficult to justify because the "foreign guest" species may have adaptive advantages over local species which otherwise would have colonised the ricefields. On such grounds we conclude that any modern environments subject to substantial human influence should be used only with caution for palaeoecological interpretations. Since truly unspoiled habitats are rare on our planet this caveat has considerable scope. And it would be equally dangerous to interpret the faunas of ancient environments (other than any actual fossils that might occur) on the basis of the similarity of their substrate characteristics to those of some modern environments.

Thirdly, the work of Tetart (1975, 1978) suggests a recently activated cytological pathway by which sexually thelytokous parthenogenetic populations first achieve chromosomal polymorphism within demes at the same locality and then with splitting and isolation of these demes evolve with time into new parthenogenetic races and species, such as we find, for example, in European *Isocypris*.

Fourthly, the species listed in Table 2 seem to form a group which turns up again and again in ricefields assemblages. The genera listed in Table 2 comprise most of the known ospiti esteri; others include such genera as Zonocypris and Cyprilla (Singh, 1971). It will be interesting to see how many of them occur in regions which have yet to be studied for their ricefields ostracodes, such as the southern United States and Australia.

We noted in an early section that our concept of *ospiti esteri* might well be of more general significance in helping to interpret parthenogenetic distribution patterns. Having worked through our exemplar group in some detail, we end by suggesting that the

conclusions listed above seem applicable to all groups of lower crustaceans with minute desiccation-resistant eggs and a capacity for both amphigonic and parthenogenetic reproduction.

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