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Ligia simoni: A Model for the Evolution of Terrestrial Isopods

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Summary. Most species of the isopod genus *Ligia* live on rocky sea-shore. Some species have conquered terrestrial biotopes in mist-forest on steep and isolated mountain-ridges adjacent to the sea. The ecological situation of one of these — *Ligia simoni,* which has been collected by the author on the Sierra Nevada de Santa Marta in Colombia — and its transition from marine to terrestrial habitats is analysed. It is taken as a model to reconstruct the initial steps of the conquest of land by isopods.

Zusammenfassung. Die meisten Arten der Isopoden-Gattung *Ligia* bewohnen felsiges Meeresufer. Einige Arten haben terrestrische Biotope in Nebelwäldern an steilen und isolierten Gebirgshängen erobert, die in unmittelbarer Nachbarschaft des Meeres gelegen sind. Die ökologische Situation einer dieser Arten — *Ligia simoni,* die vom Autor auf der Sierra Nevada de Santa Marta in Kolumbien gesammelt wurde — und ihr Übergang von marinem zu terrestrischem Habitat wird analysiert. Sie wird als Modell genommen, um das Anfangsstadium der Landeroberung durch Isopoden zu rekonstruieren.

A. Introduction

Terrestrial isopods (Oniscoidea), derived from marine ancestors, today populate with more than 1500 species terrestrial biotopes all over the world from the sea-shore to real desert habitats. A number of authors have dealt with their transition from marine to terrestrial environment and with their adaptations to life on land (for literature see Warburg, 1968). These authors have been mainly occupied with the investigation of physiological adaptations. In the present paper the evolution of terrestrial isopods will be discussed from the viewpoint of evolutionary ecology.

In 1974 I had the opportunity to collect a number of terrestrial isopods on a field trip up the San-Lorenzo-promontory of the Sierra Nevada de Santa Marta in Northern Colombia. A sample taken in the mist forest at about 1600 m a. s. l. contained, among „normal" terrestrial isopods, a species of *Ligia*. The members of this genus are usually confined to the supralitoral zone of rocky sea-shore, which they inhabit all over the world with about 20 species. Five species, however, have been found high up in the mist forest zone in tropical regions: *L. perkinsi* in Hawaii, *L. simoni* and *L. platycephala* in Northern South America, *L. philoscoides* on a Polynesian island and *L. latissima* on New Caledonia (compare JACKSON 1922 and 1939, VANDEL 1952). The specimens which I collected on the Sierra Nevada de Santa Marta proved to belong to *Ligia simoni*. This species was collected at the same locality in 1913 and described by PEARSE (1916) under the name *L. richardsonae*, which proved to be a synonym of *L. simoni* (see VANDEL 1952, p. 81). *Ligia simoni* was originally described from the Cumbre de Valencia in Venezuela at about 1200 m a. s. l.

A re-description of this insufficiently described species will be given in a separate paper.

I wish to thank Dr. F. KÖSTER (Santa Marta, Colombia) to whose biological enthusiasm I owe the opportunity to participate on a excursion to the San-Lorenzo-promontory during which I could collect the isopod material dealt with in the present paper; Dipl. Biol. U. HÄUSSLER (Tübingen) for critical discussions on evolutionary ecology and the question of physiological limitations; Dr. D. SCHLEE (Ludwigsburg) for a critical reading of the manuscript; and Dr. F. FERRARA (Florence) for informations on sand-beach communities in Somalia.

B. Ecological observations

The biotope in which *Ligia simoni* was found is montane primary mist forest at about 1400 m a. s. l. The terrain consists of steep slopes with a dense cover of jungle where the dominating plants are tree-ferns, lianas, tree-climbing philodendron, and trees with a host of epiphyts (mainly bromeliads). Small brooks are running down the slopes about every 100 m in horizontal section. The ground in the open parts at the roadside was covered with a dense herbaceous vegetation except for very steep parts where permanent erosion did not allow any plant growth. The daily mist provides a micro-climate on or near the ground with a permanently saturated or nearly saturated moisture. *Ligia simoni* was found under logs and stones in the herbaceous vegetation at the roadside. It was associated with two other isopods, *Synarmadillo ruthveni* (Pearse, 1916) and *Scleropactes colombiensis* (Pearse, 1916). Both of these species are conglobating forms with relatively slow movements, whereas *Ligia simoni* is a swift non-conglobating type. PEARSE, when collecting in 1913 at the same location, had also found these three species associated.

The Sierra Nevada de Santa Marta is an isolated part of the Eastern Cordillera rising directly from the shore of the Caribbean Sea to about 5800 m a. s. l. at a distance of only 45 km from the shore. In the surroundings of the town Santa Marta there is a dry coastal plain (cactus steppe) of a few km width stretching out between the wooded slopes of the promontory and the sea-shore. Further to the northeast (e. g. in the Tayrona Park), however, the forested slopes of the promontories are running right down to the sea-shore. For further details on morphology, climate and history of the Sierra Nevada see, for instance, ADAMS 1973.

C. Discussion of evolutionary ecology

The species of *Ligia* are „normally" inhabitants of rocky sea-shore. Their nutritional basis ist the marine growth in the spray-zone (mainly algae), which the animals „graze" off with their cutting mouthparts. To escape too heavy predation (main predators are birds and crabs) two different strategies have been developed. The one, practiced for example by *Ligia italica* from the Mediterranean Sea, ist the development of an effective locomotory system (long legs and well-developed muscular apparatus) to allow swift movements, connected with a highly efficient optic apparatus. This allows early recognition of predators and „high-speed" running abilities to retreat to a crevice or into the water. The other strategy is the „clinging-behavior" practiced, for example, by *Ligia oceanica* from the European Atlantic coast. In this case the animal, when threatened, presses itself into a groove on the uneven rock surface, with the lateral doublures (epimera) of the flat tergites tightly fitting to the rock-surface. This has two advantages: first it is not easy to detect the animal in this position (no shadows, greenish-grey protective coloration!) and if it is detected the predator will have great difficulties to pick it off the substrate with a pincer-like instrument (bird's bill, chela of a crab) (compare Schmalfuss 1975). These two strategies seem to be correlated with the climate of the distribution area, the first one is practiced by species inhabiting tropical and subtropical regions, the second one by species from temperate zones.

This is the ecological situation of those species of *Ligia* inhabiting the seashore. The terrestrial species of *Ligia* (see chapter A) all inhabit mist forest in tropical regions situated on steep mountain sides rising directly from the sea. In all cases the biotope is, to a smaller or greater degree, isolated from other comparable biotopes, has a restricted extension and is due to geologically recent events (volcanic activity on Hawaii and New Caledonia, late Tertiary orogenetic activity in Northern South America).

From this situation it is easily perceptible that only small physiological changes were needed for these species to switch from the sea-shore environment to the mist forest. The nutritional basis remains the same or nearly the same in the mist forest, the permanently saturated moisture allows growth of algal films everywhere in this environment. The „anti-predation-strategy" also remains the same (the terrestrial species of *Ligia* belong to the long-legged type), the running abilities could even be reduced because of more sheltered habitats (under stones, logs etc.). Only the osmotic regulation had to be changed to adjust to the hypotonic milieu. The „reason" for the conquest of this terrestrial biotope has, however, to be seen in the fact that there was an empty niche (created by recent climatic and geological events) the primary basis of which is always a nutritional one, and that because of the isolated situation there were no competitors already better adapted to this niche.

Now *Ligia simoni* is, in this discussion, an especially interesting example. This is because today at the sea-shore from where the species must have invaded the terrestrial biotope, neither this nor another species of *Ligia* is present. The author has had the opportunity for a brief study of the sea-shore communities in this region, and from this experience the reason for the absence of *Ligia* became evident. The rocky parts of the shore, where *Ligia* should be expected, were densely populated with the crab *Grapsus grapsus*. This crab uses the same food-source as the shore-species of *Ligia* do, it is a grazer of marine growth in the spray-zone, and it also uses crevices to retreat from predators. Additionally it is a predator on small arthropods. Concerning the food source it is a good example for the rule that with a higher and more stable primary production (constant high temperature) larger consumers can sustain themselves on a given food source.

So being a superior competitor and a possible predator on *Ligia* and using exactly the same micro-habitats these dense populations of *Grapsus* inevitably lead to the extinction of *Ligia* in this biotope, in spite of the „antipredation"-strategies described above. A comparable situation is found on sand-shore biotopes in Somalia, where dense populations of the ghost-crab *Ocypode* are present and the sand-beach isopod *Tylos* is missing (Ferrara pers. comm.). Before *Ligia* was extinguished at the shore by *Grapsus* it obviously „had the opportunity" to „escape" up into the mountainous mist forest. This statement has, of course, not to be taken literally, by all probability *Ligia* would also have conquered the terrestrial biotope if its existence would not have been threatened at the sea-shore, as the example of *Ligia perkinsi* from Hawaii demonstrates where a shore-species, *L. hawaiensis*, is present which is closely related, perhaps conspecific with *L. perkinsi*. But this fact of being extinguished at the shore may have greatly accelerated the process of adaptation to the terrestrial biotope. Otherwise the shore-population, with its selection-pressure for the shore-biotope, would have contributed gene-material to the common gene-pool (at least for the initial stage of this process a continuous gene-flow has to be postulated) which would have been adversary for the adaptation to terrestrial life. In this case the species would have had to „wait" until some external isolating factor would have separated the two populations, so that each could effectively adjust to its specific selection-pressure.

The conquest of terrestrial biotopes by *Ligia* is a secondary step considering the conquest of land by isopods, and it will probably not have great evolutionary consequences, since the niches to which a further terrestrial adaptation could lead are already occupied. They are occupied by species which originated from the first land-ward step of the isopods which must have taken place much earlier, probably some time in the early Mesozoic. But this example of *Ligia* enables us to visualize an early stage of this first „terrestrialization" of isopods. It points out the conditions under which this conquest of the land possibly started. The terrestrial isopods (Oniscoidea), by all probability, originated from marine forms (for various reasons not to be discussed here). If we allow the case of *Ligia* to stand as a model for the first wave of isopods towards terrestrial biotopes, it shows that this process most probably took place in tropical regions, with rain forest or mist forest adjacent to the sea-shore which allowed an easy transition without the demand of great sudden physiological changes. From these biotopes there is no difficulty to imagine a further invasion of drier habitats step by step (today isopods inhabit even deserts), since there exist all sorts of transitional habitats. And this example also shows us that it is highly doubtful whether physiological „limitations" can keep off organisms from conquering new biotopes, given a nutritional basis not already taken over by competitors, a graded transition from the old to the new biotope, and enough time to adjust physiologically and morphologically to the new conditions.

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