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Morphology and Function of Cuticular Micro-Scales and Corresponding Structures in Terrestrial Isopods (Crust., Isop., Oniscoidea)*

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Summary. In nearly all terrestrial isopods the cuticle of the tergites is equipped with scale-like, circular or polygonal micro-ridges, whereas in aquatic isopods the cuticle is smooth. Brief descriptions of the microscopic cuticle surface and corresponding SEM photographs are given for 16 isopod species. The function of these structures is considered to be 'anti-adhesive', preventing small wet substrate particles from sticking to the cuticle, by minimizing the possible contact area. Particles sticking to the cuticle would hinder the animal's freedom of movement and would prevent a free exchange of water and oxygen between cuticle and environment. The occurrence of the structures as well as the differences in their morphology may be explained by ecological and behavioral differences in the corresponding species.

Zusammenfassung. Bei fast allen Land-Isopoden weist die Kutikula der Tergite schuppenförmige, ringförmige oder polygonale Substrukturen auf, während sie bei aquatischen Isopoden glatt ist. Für 16 Isopodenarten wird eine kurze Beschreibung der Mikro-Skulptur der Kutikula-Oberfläche gegeben und durch entsprechende REM-Aufnahmen dokumentiert. Funktionell werden diese Strukturen als „Anti-Adhäsions-Einrichtungen" interpretiert; sie verhindern durch Kontaktflächen-Minimalisierung ein Festkleben von feuchten Substrat-Partikeln auf der Kutikula-Oberfläche. Solche festklebenden Partikel würden die Tiere in ihrer Beweglichkeit einschränken und einen freien Austausch von Sauerstoff und Wasser zwischen Kutikula und Außen-Milieu verhindern. Das Vorhandensein oder Fehlen sowie die Verschiedenheiten in der morphologischen Ausprägung dieser Strukturen können durch ökologische und Verhaltens-Unterschiede bei den entsprechenden Arten erklärt werden.

A. Introduction

While investigating the morphology and functional aspects of cuticular structures in crustaceans, I realized that in nearly all terrestrial isopods scale-like, circular

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or polygonal cuticular microstructures are present on the tergites, whereas in aquatic isopods the surface of the tergal cuticle is smooth. This difference between terrestrial and aquatic forms and previous functional hypotheses on cuticular structures of terrestrial isopods (Schmalfuss, 1977a) lead to a functional interpretation which accounts for the morphology and distribution of the scale-like microstructures and is consistent with the ecological and behavioral situation of these animals.

This paper presents a part of the results of a research program on the constructional morphology of cuticle structures in recent and fossil arthropods, conducted and financed by the Sonderforschungsbereich 53 at the Institut und Museum für Geologie und Paläontologie, University of Tübingen (FRG).

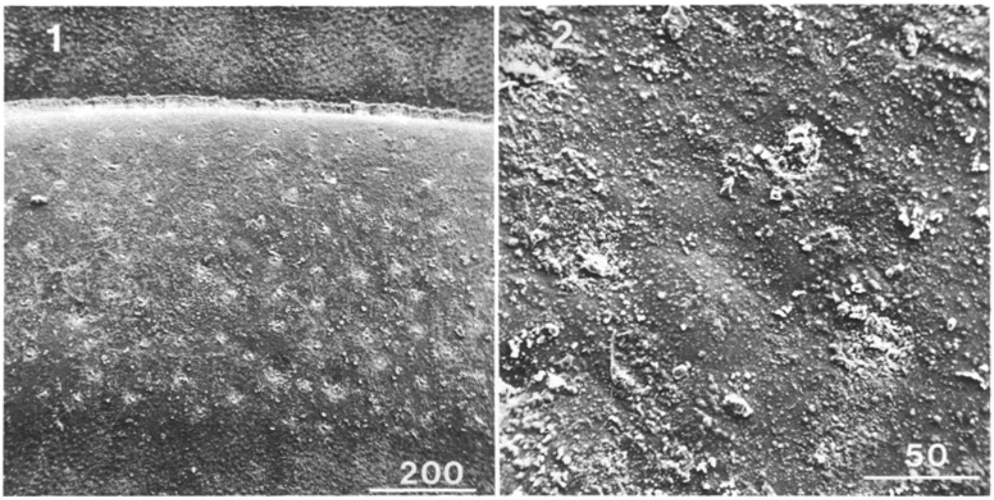
B. Previous Investigations

The presence of a scaly microstructure on the tergites of terrestrial isopods has often been mentioned, and some authors have studied these structures in detail (e.g., Herold, 1913). Recently, Holdich and Lincoln (1974) published a SEM investigation of cuticular structures in *Porcellio scaber*. Their paper contains some excellent SEM photographs and detailed descriptions of four types of micro-scales (called ‚plaques' by these authors) found in *Porcellio scaber*. However, neither Holdich and Lincoln nor the earlier authors have attempted any functional interpretation of the micro-scales and corresponding structures.

C. Material and Methods

Except for *Armadillo tuberculatus* which was collected by Dr. H. Pieper and *Lanceochaetus camerunicus* collected by Dr. E. Kohler, the isopod material used in the present study was collected by myself. My personal isopod collection is now in the possession of the Staatliche Museum für Naturkunde, Stuttgart, in the following list, therefore, the museum numbers are given of the samples from which the specimens were taken for SEM-investigation (SMNS = Staatliches Museum für Naturkunde Stuttgart, isopod collection number).

Species investigated:
a. Sphaeroma serratum (Fabricius, 1787), Flabellifera, Sphaeromatidae (SMNS 1018): island of Karpathos, Aegean. – *b. Tylos latreillei* (Audouin, 1825), Oniscoidea, Tylidae (SMNS 1548): island of Astipalea, Aegean. – *c. Hyloniscus beieri* (Strouhal, 1954), Oniscoidea, Trichoniscidae (SMNS 1605): Olymp, Greece. – *d. Cretoniscellus aegaeus* (Schmalfuss, 1972), Oniscoidea, Trichoniscidae (SMNS T 1247): Crete. – *e. Haplophthalmus montivagus* (Verhoeff, 1941), Oniscoidea, Trichoniscidae (SMNS 4039): near Tübingen, Southern Germany. – *f. Oniscus asellus* (Linnaeus, 1758), Oniscoidea, Oniscidae (SMNS 4060): Tübingen. – *g. Platyarthrus hoffmannseggi* (Brandt, 1833), Oniscoidea, Platyarthridae (SMNS 4041): near Tübingen. – *h. Trichorhina tomentosa* (Budde-Lund, 1893), Oniscoidea, Platyarthridae (SMNS 4035): a greenhouse, Tübingen. – *i. Lanceochaetus camerunicus* (Schmalfuss and Ferrara, in press), Oniscoidea, Platyarthridae (SMNS T 8257): Victoria, Cameroon. – *j. Porcellio scaber* (Latreille, 1804), Oniscoidea, Porcellionidae (SMNS 4054): Tübingen. – *k. Porcellionides pruinosus* (Brandt, 1833), Oniscoidea, Porcellionidae (SMNS 4057): a greenhouse, Tübingen. – *l. Armadillidium granulatum* (Brandt, 1833), Oniscoidea, Armadillidiidae (SMNS 1219): Crete. – *m. Orthometopon phaleronense* (Verhoeff, 1901), Oniscoidea, Trachelipidae (SMNS 1517): near Athens, Greece. – *n. Orthometopon dalmatinum* (Verhoeff, 1901), Oniscoidea, Trachelipidae (SMNS 1605): Olymp, Greece. – *o. Hemilepistus reaumuri* (Audouin, 1825), Oniscoidea, Tracheli-



Figs. 1 and 2. *Sphaeroma serratum*, surface of peraeon tergite (scale in μm)

pidae (SMNS 8019): Kebili, Tunisia. – *p. Armadillo tuberculatus* (Vogl, 1876), Oniscoidea, Armadillidae, (SMNS 1509): Greek island, Kithira.

For the SEM investigation the specimens, being fixed in 70% alcohol, were air dried, coated with gold palladium and studied with and photographed from a 'Stereoscan' (Cambridge Instrument Ltd.).

D. Results

I. Morphology and Ecology

1. Aquatic Isopods

a and b) Sphaeroma serratum. This species illustrates the situation in aquatic isopods. The tergites bear no regular micro structures (Fig. 1), the irregular structures seen at higher magnification (Fig. 2) are probably the result of the calcification process and of abrasion. The species is able to roll up into a perfect ball; it lives on marine pebble-beaches at the waterline. The same tergite surface has been found in species of *Idotea* (Valvifera, Idoteidae; marine) and in *Tylos latreillei* (Oniscoidea, Tylidae; living above the waterline on marine sand beaches).

2. Terrestrial Isopods

c) Hyloniscus beieri. The tergites are equipped with scales arranged like tiles on a roof (Fig. 3). The species lives in the moist leaf litter of deciduous forest.

d) Cretoniscellus aegaeus. The tergites bear longitudinal ridges, like all the Haplophthalminae (functional interpretation see Schmalfuss, 1977a). The sur-

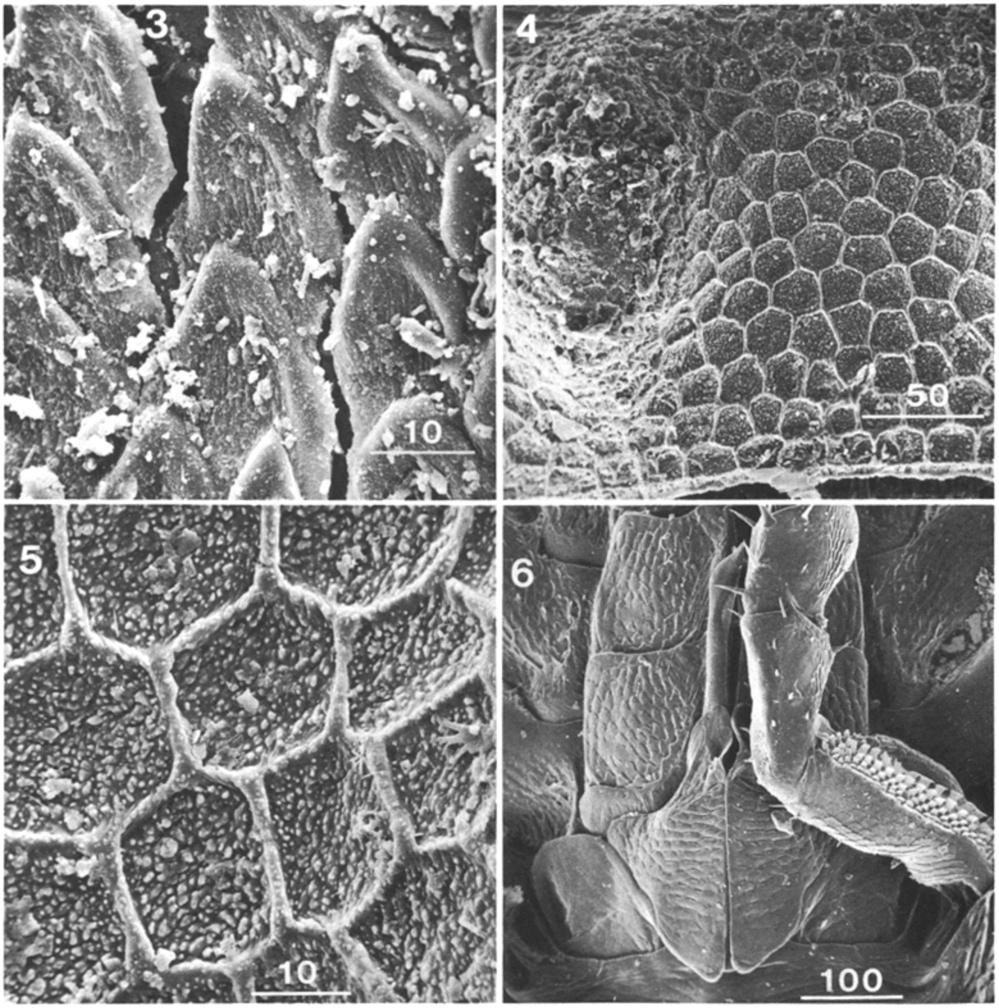
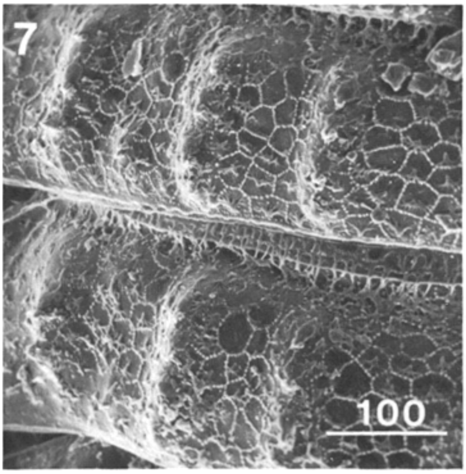


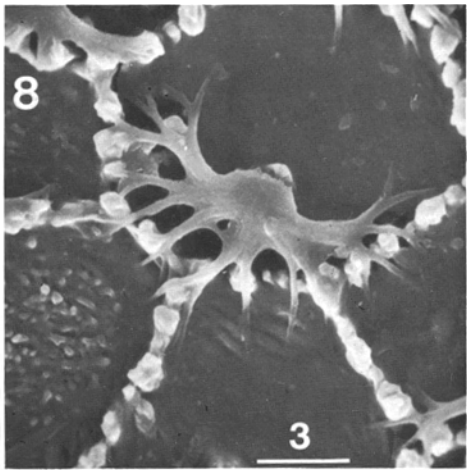
Fig. 3. *Hyloniscus beieri*, scaly microstructures on peraeon tergite

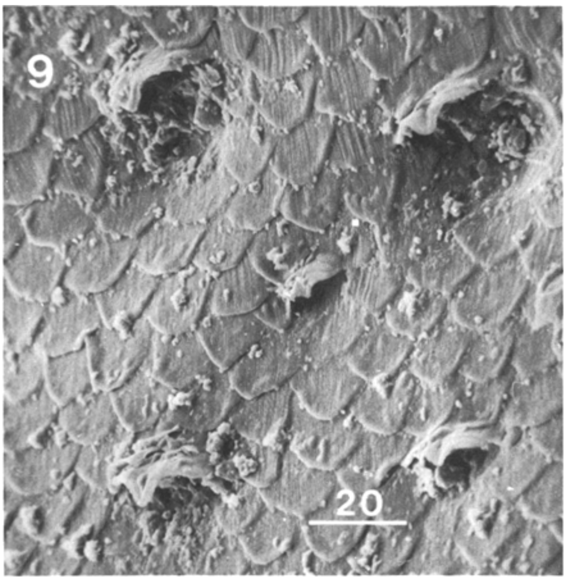
Figs. 4 and 5. *Cretoniscellus aegaeus*, polygonal micro-ridges on peraeon tergite

face of the ridge crests is without regular microstructures, the concave surface between the ridges is covered with a polygonal pattern of secondary ridges with a height of about 1 µm (Figs. 4 and 5). The species is, up to now, only known from the type series, which was found *in* the water of a rock pool in the otherwise dry bed of a river. It can however be assumed that the species also lives in moist litter substrate or in caves as all other Haplophthalminae do.

e) Haplophthalmus montivagus. The longitudinal primary tergite ridges resemble those in the previous species (though of a different morphological type, see Schmalfuss, 1977a) and have a comparable polygonal pattern of secondary ridges between the primary ones (Fig. 7). Additionally, at least in juvenile





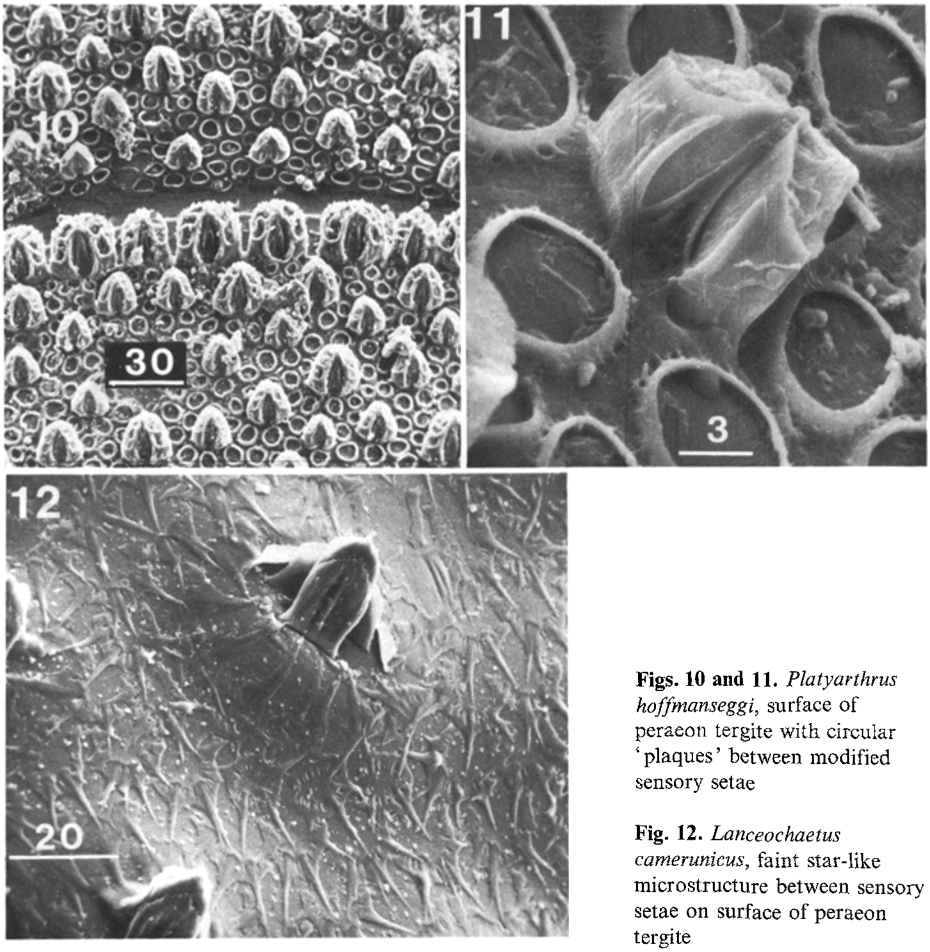


Figs. 6–8. *Haplophthalmus montivagus*, Fig. 6 ventral view of abdomen of male showing scaly microstructures on the surface of the pleopod-exopodites, Figs. 7–8 newly hatched juvenile (manca stage) of about 1 mm length with polygonal micro-ridges and associated antler-like structure on peraeon tergite

Fig. 9. *Oniscus asellus*, scales on peraeon tergite

specimens, a peculiar antler-like structure has been found in the center of each polygonum. The processes of this structure are bent over and fixed to the caudal part of the polygonal ridges (Fig. 8; compare also Schmalfuss, 1977a, p. 160). It could also be shown in this species that even the flat parts of the ventral appendages, i.e., the pleopod-exopodites and the coxopodites of the peraeopods, have a cuticle with a scaly microstructure (Fig. 6). The species lives in wet deep leaf layers of deciduous forest.

f) Oniscus asellus. A pronounced scale-like pattern of microstructures shows between the sensory scale-spines (Fig. 9). The species lives in damp places under stones and pieces of wood, etc.



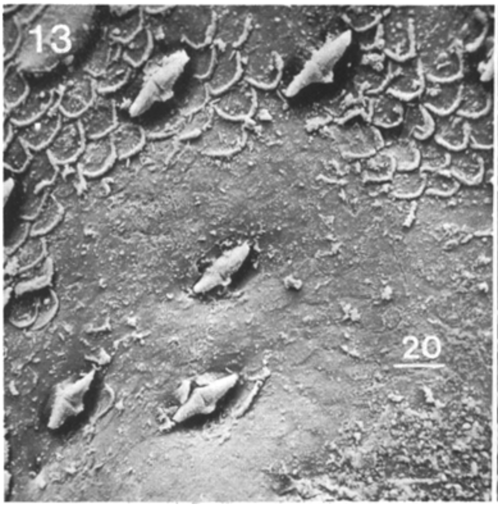
Figs. 10 and 11. *Platyarthrus hoffmanseggi*, surface of peraeon tergite with circular 'plaques' between modified sensory setae

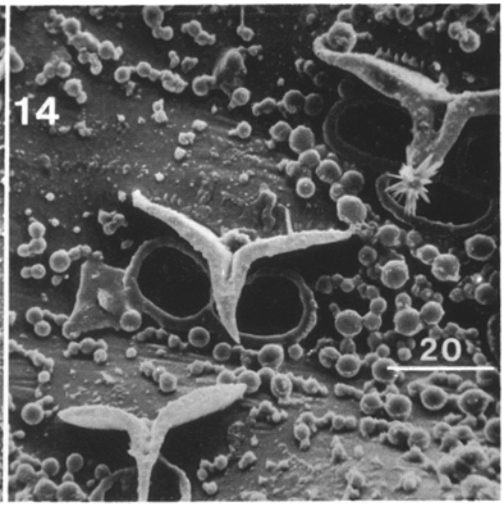
Fig. 12. *Lanceochaetus camerunicus*, faint star-like microstructure between sensory setae on surface of peraeon tergite

g) Platyarthrus hoffmannseggi. Microstructures consisting of isolated circular ridges are found in between the peculiar scale spines (Figs. 10 and 11, see also Schmalfuss 1977a). The species lives in ants' nests.

h) Trichorhina tomentosa. The scaly 'plaques' of the tergite cuticle are comparable to those of *Porcellio scaber* (see Schmalfuss, 1977a, p. 165). The species was found in a greenhouse under flower pots.

i) Lanceochaetus camerunicus. The microstructures corresponding to the 'plaques' of other species are only very faintly developed and consist of very low ring walls with small teeth at the inner side and long pointed processes at the outside (Fig. 12). The species is only known from the type series, which was found in a rotten tree.





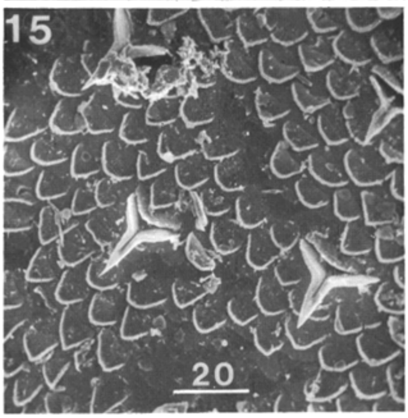


Fig. 13. *Armadillidium granulatum*, peraeon tergite with modified sensory setae and scaly micro-structure; the lower half of the photograph is part of a tubercle the surface of which is without scales

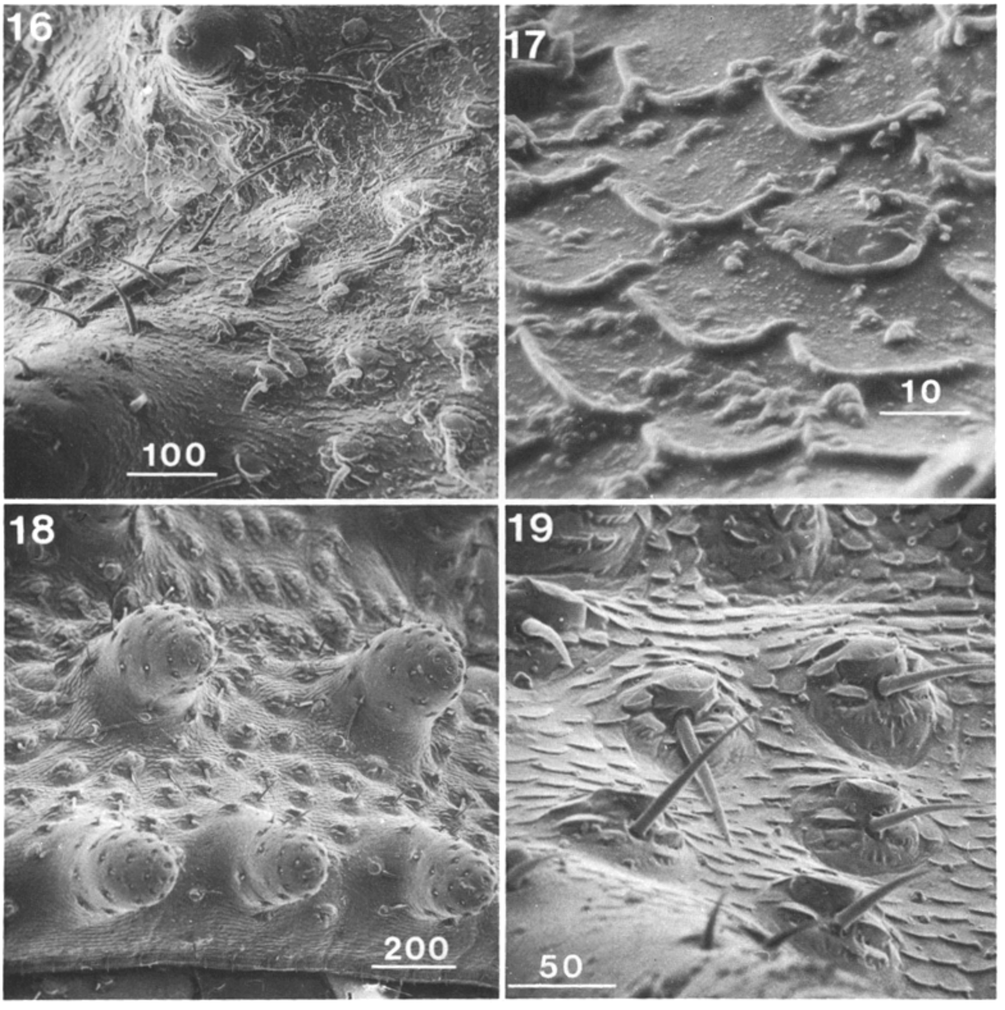
Fig. 14. *Orthometopon phaleronense*, peraeon tergite with sensory setae ('tricorns') and wax secretions

Fig. 15. *Orthometopon dalmatinum*, peraeon tergite with sensory setae and micro-scales

j) Porcellio scaber. Scale-like 'plaques' are present as described and figured extensively by Holdich and Lincoln (1974). The species lives in damp places under stones, pieces of wood, in cellars, etc.

k) Porcellionides pruinosus. No scaly microstructures are present; the tergites, however, produce waxy secretions which form circular walls at the caudal side of each tactile seta ('tricorn' of Holdich and Lincoln) and chains of small balls between the setae. These structures have been investigated, among others, by Ermin (1944). They correspond exactly to those structures figured here for *Orthometopon phaleronense.* The species inhabits even very dry biotopes with a semidesert climate.

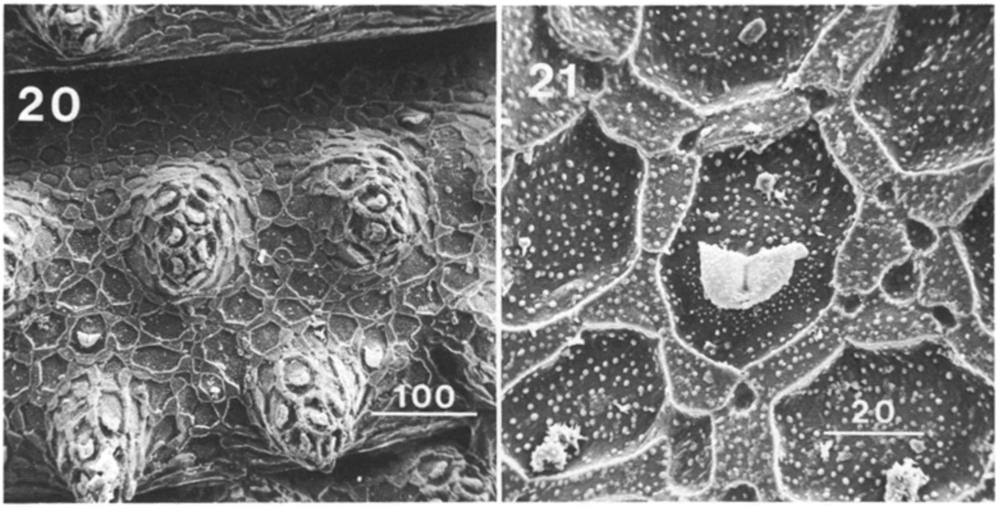
l) Armadillidium granulatum. Scale-like 'plaques' are distributed in the areas between the macroscopic tergal tubercles. The cuticle on the tubercles has no scaly microstructures (Fig. 13). The species, with a mediterranean distribution, inhabits dry biotopes in the neighborhood of the sea.



Figs. 16–19. *Hemilepistus reaumuri*, surface of peraeon cuticle, with tubercles, sensory setae, and micro-scales; Figs. 18 and 19 taken from an individual immediately after molt showing that the sensory setae break mechanically through the outer layer of the cuticle to the surface

m) Orthometopon phaleronense. Scale structures are absent, but waxy secretions occur as described for *Porcellionides pruinosus* (Fig. 14). The species inhabits dry Mediterranean biotopes.

n) Orthometopon dalmatinum. Scales are present (Fig. 15), corresponding morphologically to those of *Porcellio scaber*. The species inhabits woods in Southeastern Europe.



Figs. 20 and 21. *Armadillo tuberculatus*, juvenile specimen, peraeon tergite with pronounced tubercles, polygonal micro-ridges and butterfly-like sensory setae

o) Nagurus aegaeus. In the original description (Schmalfuss, 1977b) some SEM photographs are given of the tergal cuticle, which show scaly plaques corresponding to those of the preceding species. This species was found in the leaf litter around a spring on an Aegean island.

p) Hemilepistus reaumuri. Scales similar to those of *Porcellio scaber* are present (Figs. 16–19). No scales are present on the tergal tubercles. The species occurs in Northern Africa in sandy semideserts, where it spends the daylight hours and rears its young in the holes (see Linsenmayr and Linsenmayr, 1971) it digs.

q) Armadillo tuberculatus. The microstructure consists of a network of broad and somewhat irregular ridges enclosing polygonal areas at a lower level (Figs. 20 and 21). Some of these polygonal pits contain modified tactile setae (corresponding to the tricorns of Holdich and Lincoln) which have a peculiar butterfly shape in this genus and which do not surpass the 'pit-walls' in height. The walls and pits are also present on the tubercles.

3. Function

As was tentatively hinted at in a previous publication considering the network of microridges in *Haplophthalmus montivagus* (Schmalfuss, 1977a, p. 164), the function of the micro-scales and the corresponding structures is considered to be *anti-adhesive*: *these structures prevent small wet particles from sticking to the* *cuticle.* The adhesive forces of the water, and, when drying, organic or inorganic components dissolved in the water tend to cause particles to stick to the cuticle. The mechanical function of the microstructures is to *minimize* the possible *contact area.* The same mechanical function, but for the whole animal, has been attributed previously to the tergal macro-ridges occurring in many small isopods which prevent it sticking to the substrate (see Schmalfuss, 1977a). The physical aspects of the adhesive forces of water are discussed in the cited paper (p. 163): with an average height of the scale margin of 1 μm the adhesive forces of the water for a given area of contact are reduced by a factor of 4 or 5.

Particles sticking to the cuticle of the isopods would hinder the animals in their movements, the oxygen and water exchange between cuticle and environment would be suppressed, and the cuticle would be in danger of being damaged.

This functional interpretation accounts for the fact that the structures dealt with are present only in terrestrial isopods, and are missing in aquatic forms. It agrees with the fact that nearly all Oniscoidea inhabit moist micro-habitats in terrestrial biotopes, and with their cryptic behavior, hiding under stones and logs, in the leaf litter of woods, etc.

Recently, Gans and Baic described microscopic surface structures on the scales of uropeltid snakes (which burrow in most soil!). There microscopic ridge systems occur comparable to those described above for *Cretoniscellus* and *Haplophthalmus* which have, according to the authors, exactly the same function as postulated for the isopod ridges in the present paper: "The pattern inhibits wetting of the surface and adhesion of soil particles and thus reduces friction..." (Gans and Baic, 1977, p. 1348).

Among the Oniscoidea investigated four exceptions have been found, where 'plaques' or corresponding structures are missing. One is *Tylos latreillei*: the ecological situation appears to be responsible for the absence of a regular cuticular microstructure. *Tylos* is an inhabitant of sandy biotopes at the marine waterline. It lives, therefore, in permanently moist substrate which does not, however, consist of sticky humus particles but instead of clean sand: there is no danger of soft particles sticking to the cuticle. *Porcellionides pruinosus* and *Orthometopon phaleronense* have no plaques but the waxy secretions already described, which certainly function in the same way as the plaques. Indeed they may be even more efficient as 'anti-adhesive' because of their water-repelling properties. Their primary function is probably, as earlier authors have worked out, an effective means of reducing the transpiration rate of the cuticle (see., e.g., Ermin, 1944), which is a very plausible interpretation since these wax secretions occur only in species that live in very dry biotopes. Fourthly, *Lanceochaetus camerunicus* has only a very faintly developed microstructure on the tergal cuticle. Nothing is known about the behavior of this species, but it can be postulated, from the morphology of the tergal tactile setae (which have a rigid connection with the tergite and are pointing frontally!) that their micro-habitat and/or their behavior must differ from that of all other 'normal' terrestrial isopods.

The differences between the scale-like plaques and the homologous circular and polygonal structures can also be explained by correlated differences in morphology, ecological situation, and behavior. The scale-like plaques of the *Porcellio-scaber* type, with a ridge facing caudally and no steep edges at the frontal side, occur in epigaean species without pronounced tergal protuberances and with the well-developed locomotory abilities needed to avoid predators and habitats with too much or too little moisture. A frontal edge of the plaques would hinder the animals' movement through crevices, under stones, etc. In *Platyarthrus hoffmannseggi* the plaques consist of circular walls. This species has pronounced tergal protuberances (modified tactile setae), and restricted locomotory abilities. It can 'afford' these 'deficiencies' since it is an obligatory commensal in ants' nests where it is safe from most predators lurking for free-living isopods (spiders, carnivorous insects, chilopods) and where it can move about freely without needing to shelter in narrow crevices (for behavior and ecology see Janus, 1949; Mathes and Strouhal, 1954). There is evidence that one plaque corresponds to one epidermis cell (see Nemec 1895; in sections of *Hemilepistus reaumuri* the present author also found a size relation between epidermal cells and plaques. Herold (1913, p. 462) doubts this correspondence, however, without giving convincing arguments). Morphogenetically it is easier for an epidermis cell to produce a circular plaque than to construct an asymmetrical one (less differentiating information needed, law of economy). The polygonal plaque structures of the Haplophthalminae (*Cretoniscellus, Haplophthalmus*) and of *Armadillo tuberculatus* have to be seen in the same context: locomotion, is restricted in the Haplophthalminae because of their special endogaean microhabitat (see Schmalfuss, 1977a); *Armadillo tuberculatus* has perfect conglobating abilities (an effective means to avoid certain predators and to reduce transpiration rate) and correlated pronounced tergal protuberances (function, etc. see Schmalfuss, 1975, 1977a): so there is no need for a 'stream-lining' of the plaques.

In all species with tergal protuberances or macro-ridges the plaque structures are missing on these protuberances. The functional interpretation given above also agrees with this phenomenon, since the danger of substrate particles sticking to the cuticle is much greater on the concave area between the protuberances than on the convex cuticle of the tubercles or ridges. The only exception to this rule has been found in *Armadillo tuberculatus* where the micro-ridges on the tubercles have an additional function directed against predators (Schmalfuss, 1975, p. 308).

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