The terrestrial isopod genus *Schizidium* (Isopoda: Oniscidea): Systematics, distribution, morphology

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Abstract

A list of all 24 species of *Schizidium* known up to now is given, with synonyms and distribution areas. The Greek species described under *Paraschizidium* (*aegaeum*, *album*, *atticum*, *falkonerae*, *graecum*) are included in *Schizidium*. The morphological conglobation strategies of *Schizidium* are discussed and contrasted to those of *Armadillidium* and *Armadillo*. The different strategies seem to be correlated to certain biotope categories and their predator spectra.

K e y w o r d s : Isopoda, Oniscidea, *Schizidium*, systematics, distribution, functional morphology.

Zusammenfassung

Die bis heute bekannten 24 *Schizidium*-Arten werden aufgelistet, für jede Art werden Synonyme und Verbreitungsgebiete angegeben. Die griechischen Arten, die unter dem Gattungsnamen *Paraschizidium* beschrieben worden sind (*aegaeum*, *album*, *atticum*, *falkonerae*, *graecum*), werden als *Schizidium*-Arten betrachtet. Die morphologischen Einrollstrategien von *Schizidium* werden analysiert und mit denen von *Armadillidium* und *Armadillo* verglichen. Die verschiedenen Strategien scheinen mit bestimmten Biotop-Kategorien und deren Prädatoren-Spektren korreliert zu sein.

Contents

1 Introduction

In a number of families of terrestrial isopods (suborder Oniscidea) the strategy of rolling-up the body to a more or less spherical structure has been developed. This has obviously happened several times independently, judging from the systematic relationships of the families concerned (Tylidae: all genera, Synocheta: genus *Buddelundiella* Silvestri, 1897, Cinocheta: many genera). The function of this conglobation is certainly to reduce the predation rate, because in the rolled-up animal the vulnerable ventral parts are sheltered inside the ball and the outside is formed by the heavily sclerotized tergal sclerites. In species living in dry habitats there may be also the effect of reducing dehydration in the rolled-up animal, but this is certainly secondary, as "rollers" exist also in very wet biotopes and even in aquatic isopod groups (family Sphaeromatidae). The presently treated genus *Schizidium* Verhoeff, 1901 belongs to the family Armadillidiidae. All genera and species ascribed to this family are "rollers".

2 Definition of the genus *Schizidium*

The most recent definition of the genus *Schizidium* Verhoeff, 1901 was given in my publication on the Greek species (Schmalfuss 2005):

– Cross-section of pereionites semi-circular, indicating complete conglobation abilities.
– Cleft hind-corners of pereion-epimera 1 (schisma).
– Head always with frontal line, with or without lateral parts of interocular line.
– Frontal line continuous or interrupted in the middle.

This diagnosis holds true, however, for all other genera of the family Armadillidiidae possessing a schisma:

– *Eluma* Budde-Lund, 1885, distributed in southwestern Europe, with two species (Vandel 1962: 756, Cruz 1991).
– *Ballodillium* Vandel, 1961, known from Balearic island Menorca, one species (Vandel 1961).
– *Alloschizidium* Verhoeff, 1919, from Italy, Sardinia and Corsica, ten species (Taiti & Ferrara 1996).

– The Greek species of *Paraschizidium* Verhoff, 1918, which all have a schisma, while the type species *P. coeculum* (Silvestri, 1897) does not possess a schisma. Thus, either a new genus has to be erected for the Greek species, or they have to be considered to belong to *Schizidium*.

Even the tuberculated genera *Echinarmadillidium* Verhoeff, 1901, *Cyphodillidium* Verhoeff, 1939, and *Paxodillidium* Schmalfuss, 1985 may belong to this clade, having secondarily changed some of the diagnostic characters.

If the "schismatic" genera are a monophyletic group and not an example of parallel evolution, we can consider them a group that has evolved and spread along the northern shores of the Tethys Sea, with a present-day distribution from the Iberian peninsula to northern Iran. From a morphological point of view there are no possibilities to plead for sister-group relations among the genera listed above; differences in the characters as one ommatidium versus several ommatidia or a two-jointed antennula versus a three-jointed one are autapomorphies of single species or species groups inside the clade. The investigation of molecular data might help to clarify the interrelationships of the genera mentioned. For the time being I will keep those groups that are geographically separated as separate genera (*Eluma*, *Ballodillium*, *Alloschizidium*), but I ascribe the *Paraschizidium*-species described from Greece to the genus *Schizidium*. This fits from a geographical point of view, and the differences are really only size differences and allometric relations which probably have to do with body size.

3 Species presently ascribed to *Schizidium*

In the following list the species are arranged according to their distribution from west to east.

Schizidium sp., undescribed: Greece, northwestern Peloponnese, Panakhaikó Mountain, 1200 m (S. Sfenthourakis, personal communication).

Schizidium hybridum (Budde-Lund, 1896) (syn. *Armadillidium h.*): Greece, Crete and Gávdos S of Crete, and all Aegean islands SE of a line Sámos–Santoríni; Turkey, southwestern Asia Minor (Schmalfuss 2005).

Schizidium sp., affine *tinum*, ♀♀: Greece, southwestern Aegean, islet Velopúla NE of Monemvasía on the Peloponnese (Sfenthourakis 1995).

Schizidium delmastroi Schmalfuss, Paragamian & Sfenthourakis, 2004: Western Crete (Schmalfuss et al. 2004).

Schizidum falkonerae (Sfenthourakis, 1995) (syn. *Paraschizidium f.*): Greece, southwestern Aegean, islet Falkonéra W of island Mílos (Sfenthourakis 1995).

Schizidium atticum (Sfenthourakis, 1992) (syn. *Paraschizidium a.*): Greece, Attica, N of Keratéa (Sfenthourakis 1992).

Schizidium graecum (Schmalfuss, 1981) (syn. *Paraschizidium g.*): Greece, northwestern Aegean, Northern Sporades, island Lekhúsa (Schmalfuss 1981).

Schizidium album (Sfenthourakis, 1995) (syn. *Paraschizidium*

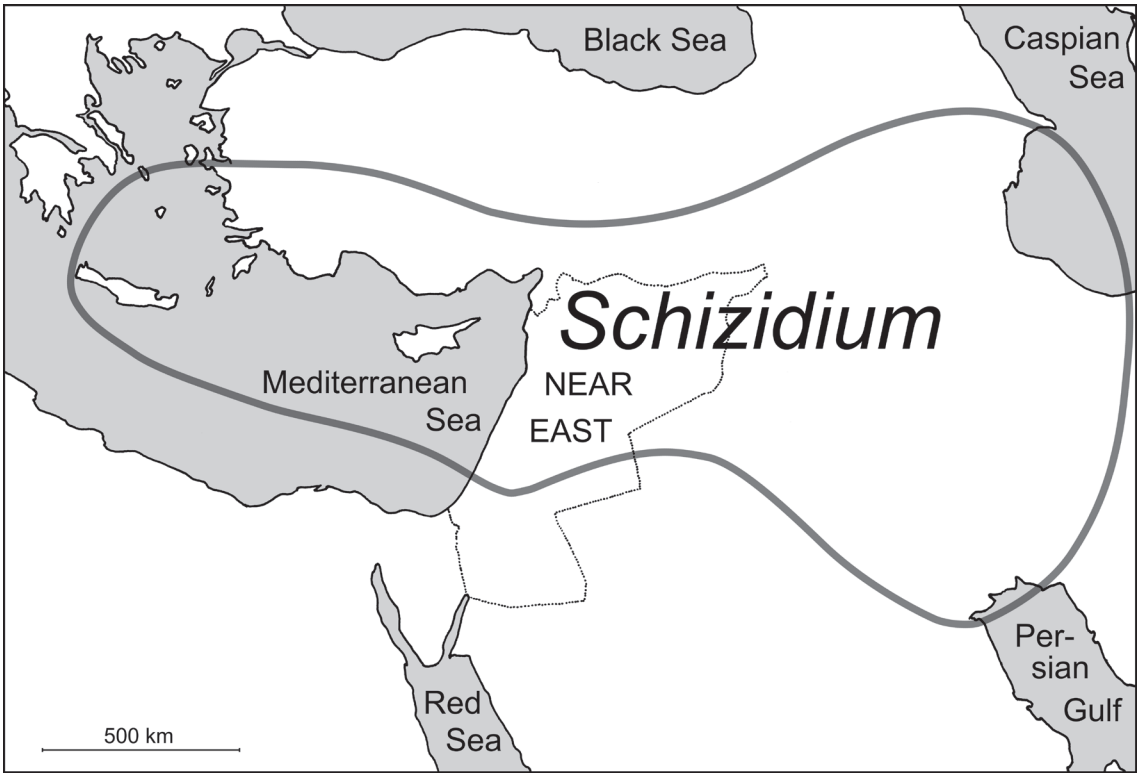


Fig. 1. Distribution area of the genus *Schizidium*.

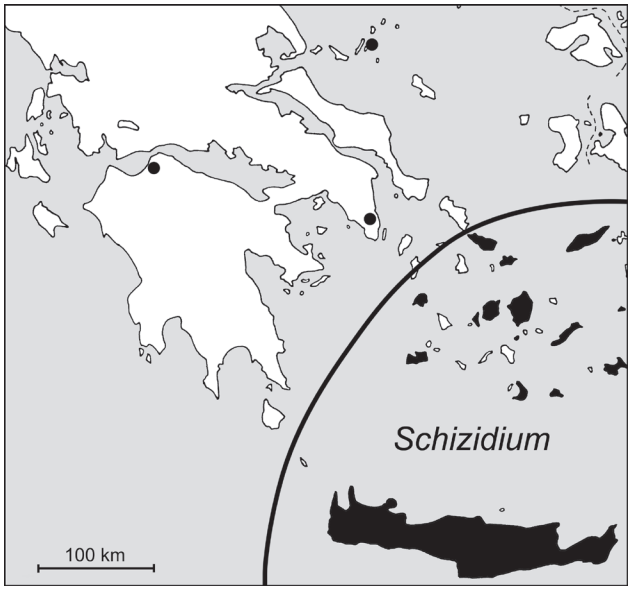


Fig. 2. The present-day distributional boundary of *Schizidium* in the Aegean region, with three relict populations on the Greek mainland and the Northern Sporades.

a.): Greece, central Aegean islands Anánes SW of Mílos, Náxos, Amorgós and Ikaría (SFENTHOURAKIS 1995).

Schizidium aegaeum (Sfenthourakis, 1995) (syn. *Paraschizidium a.*): Greece, Cyclades Islands Antímilos, Khristianí SW of Santoríni, Tínos, Míkonos and Amorgós (SFENTHOURAKIS 1995).

Schizidium oertzenii (Budde-Lund, 1896) (syn. *Armadillidium o.*): Greece, central and southeastern Aegen islands SE of a line Ikaría–Sérifos, but missing on Crete (SCHMALFUSS 2005).

Schizidium tinum Sfenthourakis, 1995: Greece, Cyclades Islands, Tínos (SFENTHOURAKIS 1995).

Schizidium schmalfussi Sfenthourakis, 1992: Greece, Aegean island Día N of central Crete (SCHMALFUSS 2005).

Schizidium perplexum (Vandel, 1958) (syn. *Cretodillium p.*): Greece, eastern Crete (SCHMALFUSS 2005).

Schizidium beroni Schmalfuss, 2005: Greece, Aegean island Santoríni (SCHMALFUSS 2005).

Schizidium paragamiani Schmalfuss, 2005: Greece, central eastern Aegean, island Fúrni (SCHMALFUSS 2005).

Schizidium osellai Schmalfuss, 1988: Western Turkey, Manisa District, Boz Dağ, above 1300 m (SCHMALFUSS 1988).

Schizidium reinoehli Schmalfuss, 1988: Western and northwestern Turkey, N of Denizli and near Bolu (SCHMALFUSS 1988).

Schizidium fissum (Budde-Lund, 1885) (syn. *Armadillidium f.*, *bifidum*): Cyprus; southern Turkey along Gulf of Iskenderun; Lebanon (SCHMALFUSS 1988).

Schizidium festae (Dollfus, 1884) (syn. *Armadillidium f.*): Lebanon (SCHMALFUSS 1988).

Schizidium tiberianum Verhoeff, 1923: Northern Israel (SCHMALFUSS 1988, 1990).

Schizidium davidi (Dollfus, 1887) (syn. *Armadillidium d.*, *Pareluma minuta*, *S. minutum*, *S. kalalae*, *Armadillidium euphrati*): Iraq, Azerbaijan (SCHMALFUSS 1988).

Schizidium rausi Schmalfuss, 1988: Southeastern Turkey, Lake of Van (SCHMALFUSS 1988).

Schizidium golovatchi Schmalfuss, 1988: Armenia (SCHMALFUSS 1988).

Schizidium persicum Schmalfuss, 1986: Northern Iran (SCHMALFUSS 1986).

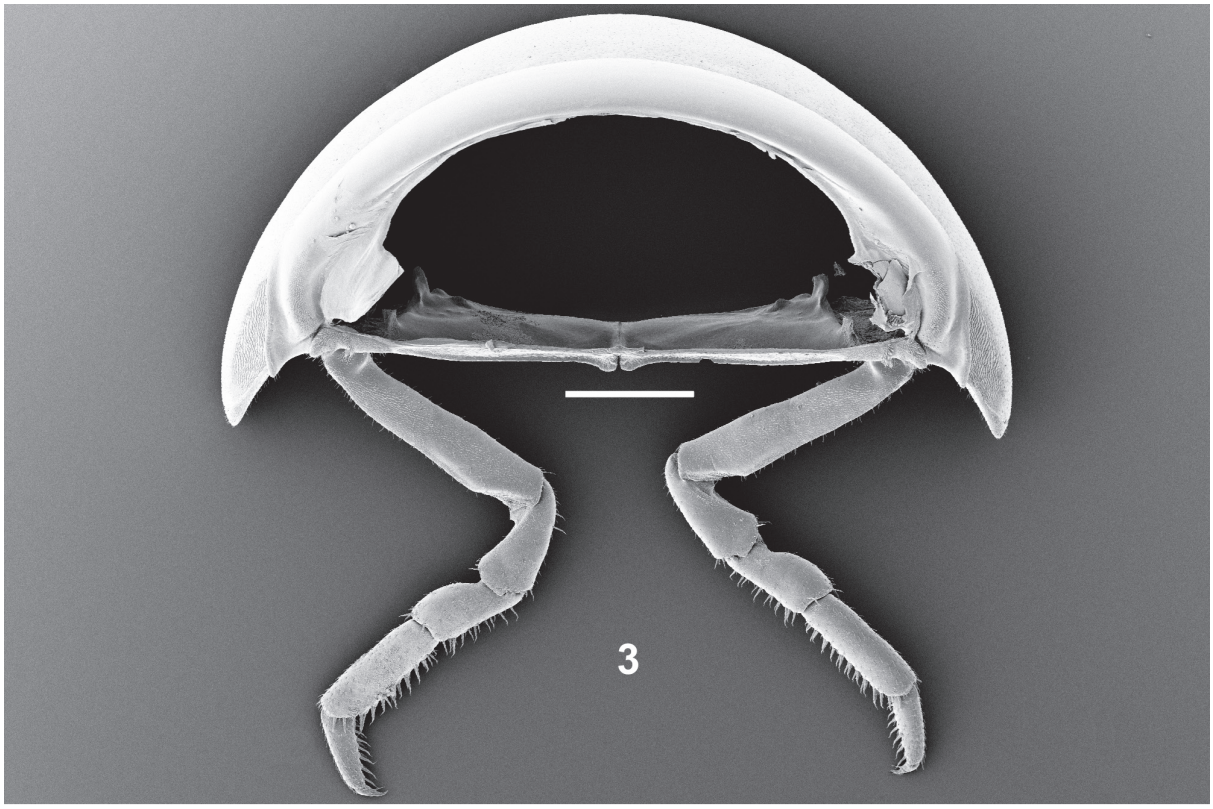
4 Distribution and ecology

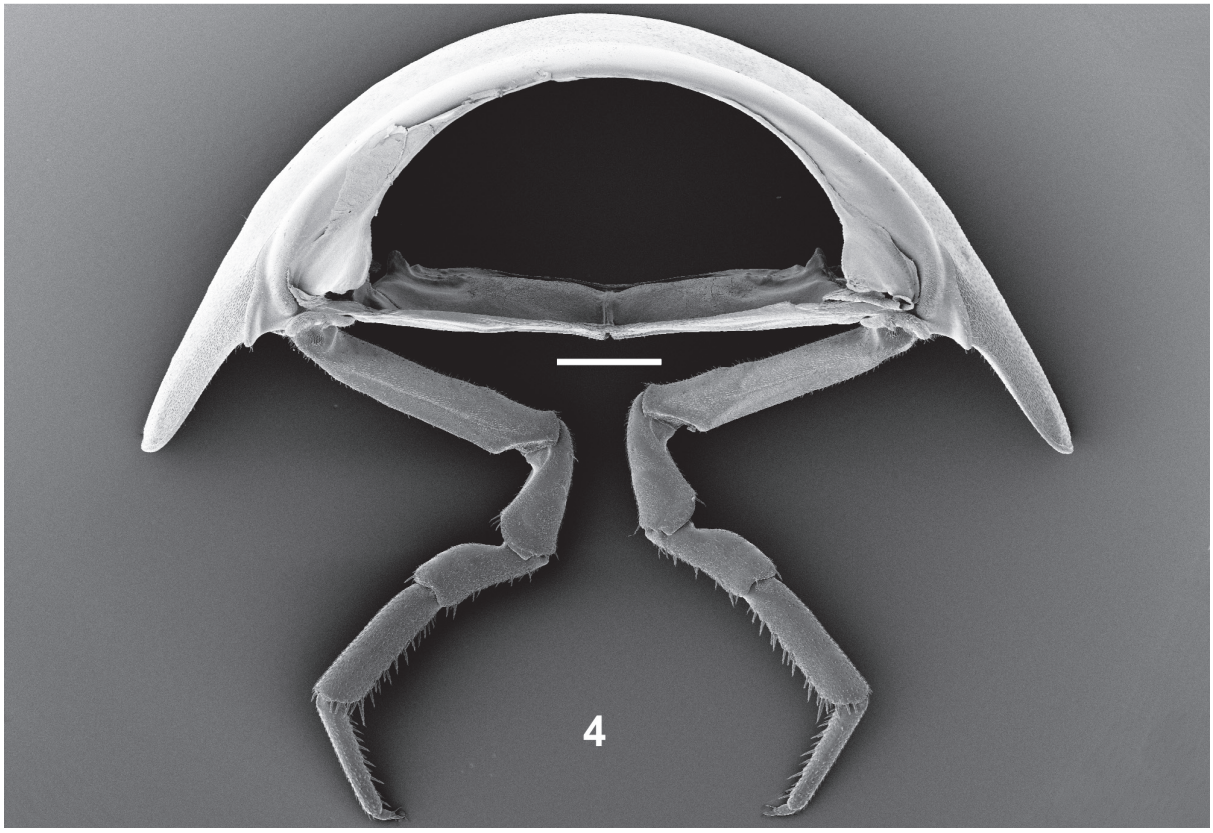
The genus *Schizidium* in the definition given above is distributed from Greece to Iran (Fig. 1). In Greece it populates most central and southern Aegean islands, west and north of that region three isolated populations have been discovered (Fig. 2). One has been found on a small island of the Northern Sporades (*S. graecum*), one on the east-central mainland in Attica (*S. atticum*) and one on the northwestern Peloponnese (*S.* n. sp., undescribed). It is tempting to interpret these three populations as relicts of a formerly more continuous distribution on the Greek mainland. Possibly the pluvial periods during the Ice Age have led to a recent immigration of competitors and predators which were formerly missing on the southern Greek mainland. The isopod genus *Armadillidium* Brandt, 1833 could be one of the competing groups. It seems that several clades of that genus have invaded the Peloponnese in recent geological times from the north, which led to a small radiation resulting in 18 species nowadays populating the Peloponnese (SCHMALFUSS 2006). This could have, in combination with changes of climate, vegetation and predator spectrum, led to the extinction of the epigean guild of the *Schizidium* species. The three relict populations found up to now are all pigmentless endogean species with reduced eyes.

On the Aegean islands three eco-morphological types of *Schizidium* species are present:

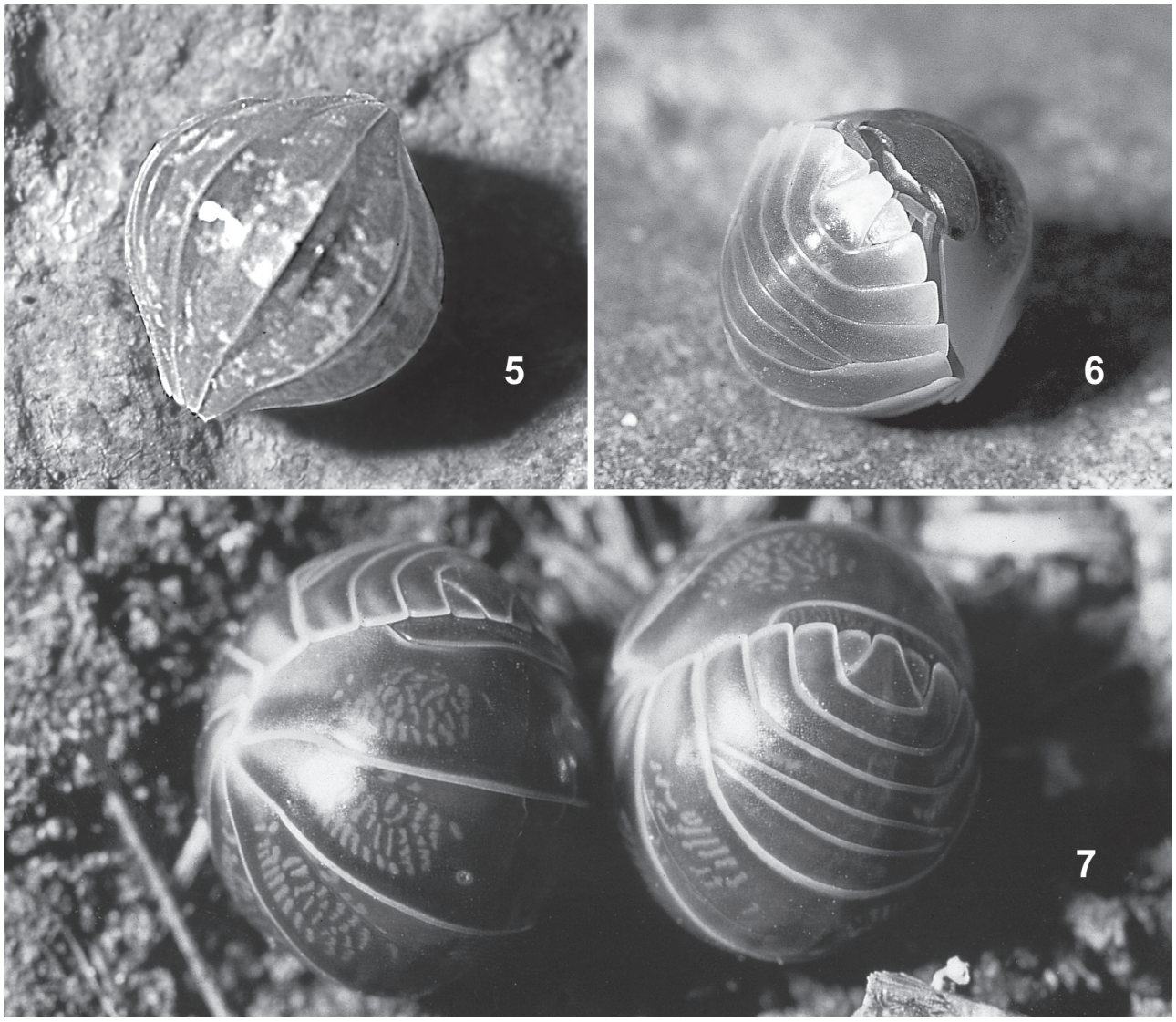
– Fully pigmented forms living an epigean way of life, hiding in daytime under stones and moving around on the soil surface in the night (*S. hybridum*, *S. oertzenii* and *S. schmalfussi*).
– Endogean species without or with reduced pigmentation and eyes, small-sized, living in crevice-systems of stony soils and normally not moving around on the open surface.
– Cave species, without pigmentation and with reduced or missing eyes, medium-sized, living in limestone cave systems (*S. perplexum* on eastern Crete and *S. beroni* on the island of Santoríni).

The fully pigmented epigean species live in open dry maquis and phrygana biotopes, where the genus *Armadillidium* occurs only with very few species, which are additionally fixed to the sea coast. On the island of Ródos *Schizidium oertzenii* is the most numerous and the biggest terrestrial isopod species – rolled-up animals reach the size of small cherries – while the three species of *Armadillidium* (*A. ameglioi* Arcangeli, 1914, *A. granulatum* Brandt, 1833 and *A. marmoratum* Strouhal, 1929, with *A. vulgare* (Latreille, 1804) missing completely on the island) are only found close to the sea-side.





Figs. 3–4. Frontal view of 3rd pereionite. – **3**. *Schizidium oertzenii*. **4**. *Armadillidium* sp. (undescribed species from northeastern Greece). – Scales: 1 mm.

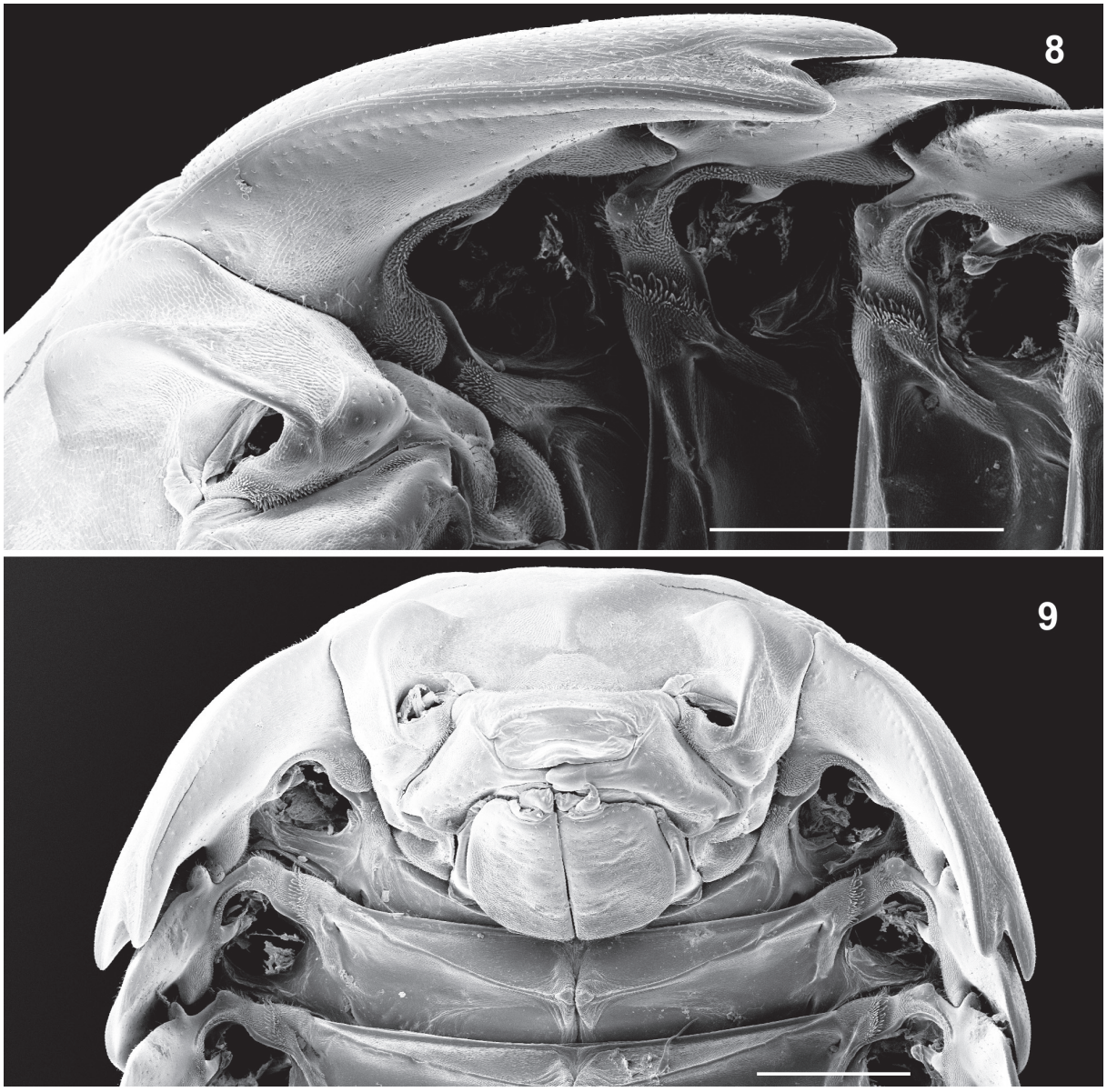


Figs. 5–7. Rolled up animals. – **5**. *Armadillidium ameglioi* Arcangeli, 1914 (Greece: Ródos Island), rolled up to a lemon-shaped ball. **6**. *Armadillidium* sp. (as Fig. 4), leaving fissures for a possible insertion of pointed appendages to inject poison into vulnerable ventral parts. **7**. *Schizidium oertzenii* (Greece: Ródos Island) rolled up to a smooth, perfectly closed "euspheric" ball.

The *Schizidium* species known up to now from western Asia are all pigmented epigean forms living in dry Mediterranean biotopes, but never venturing into semi-deserts or deserts. One species, *S. persicum*, has been found on the Elburs Mountains (northern Iran) in deciduous forest; the genus *Armadillidium* is not present in that region.

5 Morphological adaptations

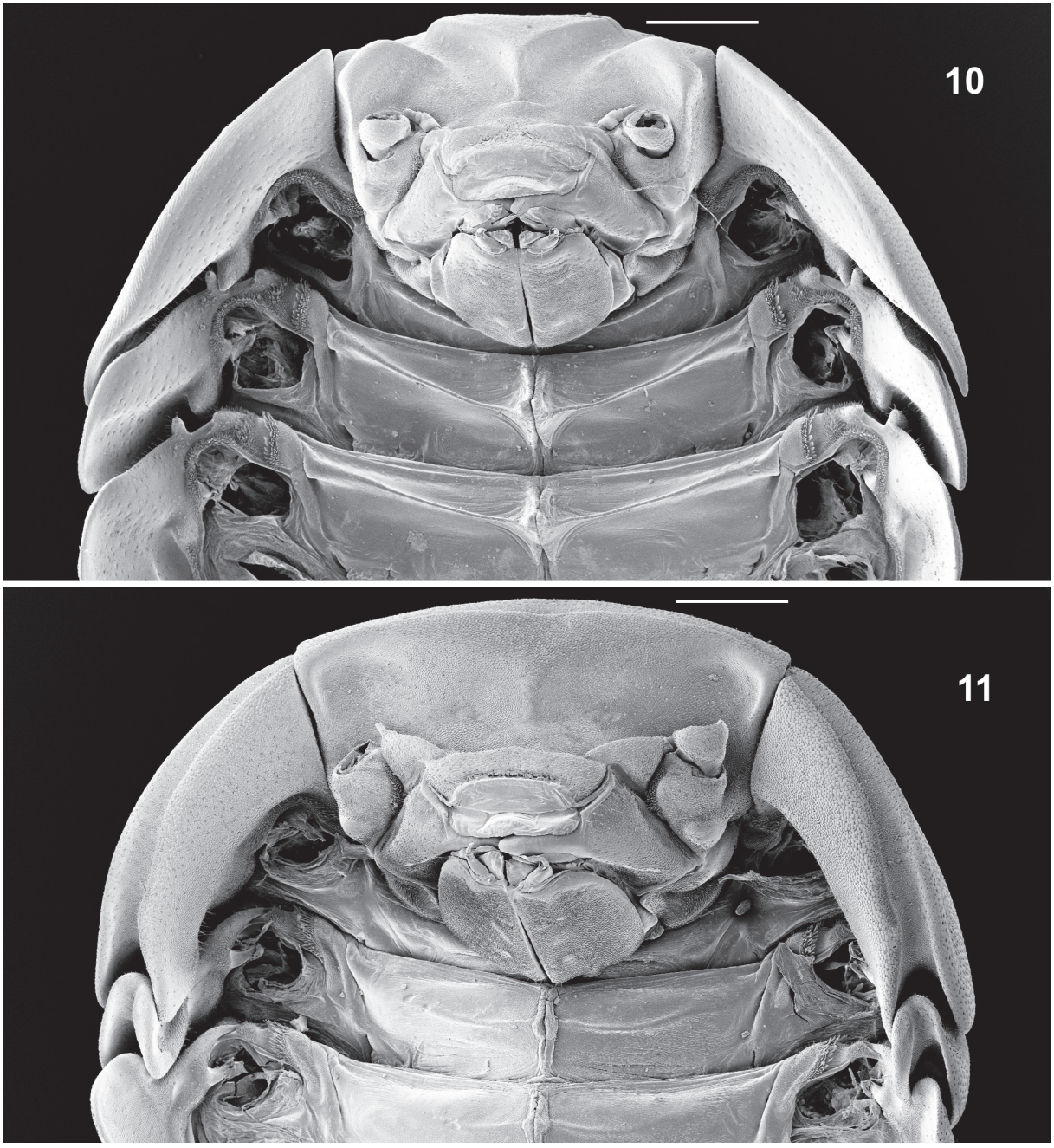
All species of *Schizidium* are able to roll up to a completely closed ball. The cross-sections of the pereion-tergites are semi-circular (Fig. 3), so the rolled-up animal is completely round ("euspheric" conglobation). This and the fact that the tergite surface is completely smooth leads to an effect which I call "flick-away principle". If any predator tries to get hold of the rolled-up animal with a pincer-like instrument (bird's bill, scorpion's pedipalp, even the jaws of lizards and small mammals) there is a good chance of the animal sliding away and rolling into some crevice where it is out of the reach of the predator. This flick-away principle applies for all euspheric isopods with smooth tergal surfaces, as e. g. for *Armadillidium vulgare* (family Armadillidiidae) and *Armadillo officinalis* Duméril, 1816 (family Armadillidae). It does not apply for tuberculated



Figs. 8–9. *Schizidium oertzenii*. – **7**. Ventral view of lateral margin of pereion-tergite 1 with schisma, left side. **8**. Ventral view of anterior pereionites. – Scales: 1 mm.

species as *Armadillo tuberculatus* Vogl, 1876 (family Armadillidae) and for species with flat epimera which roll up into a lemon-shaped structure ("pseudospheric" conglobation as in many species of *Armadillidium*, see Figs. 4, 5). The walking legs are always sheltered inside the ball, so the pseudospheric species with flatter epimera and thus a wider diameter of the pereionites can have longer legs allowing for a more rapid locomotion. The strategy to minimize predation is in this case rather to run away than to rely on the flick-away principle.

The *Schizidium* species have developed further morphological adaptations to form a completely closed ball. In the rolled-up animal the posterior parts of the abdomen are tightly covering the frontal edge of the 1st tergite and the frontal part of the head (Fig. 7). Additionally the inner side of the hind edge of the first pereion-tergite bears a process which leads to formation of a groove ("schisma", Figs. 8, 9) at the hind corner of the epimeron. In the rolled-up animal the margin of the 6th pereion-tergite is positioned in this groove, which prevents an



Figs. 10–11. Ventral view of anterior pereionites. – **10**. *Armadillidium vulgare* (Latreille, 1804). **11**. *Armadillo officinalis* Duméril, 1816. – Scales: 1 mm.

opening of the ball by shearing forces. All this results in a perfect closure of the ball, and no fissure is left that can be used by a predator to insert a pointed appendage and to inject poison into the vulnerable ventral parts (spiders, scorpions, chilopods). So this strategy seems to be directed especially against arthropod predators that overwhelm their prey by injecting venoms. In *Armadillidium* the rolled-up animal cannot be closed without leaving fissures that can be used for poisonous injections (Fig. 6), and the schisma is missing (Fig. 10), thus a predator can open the ball by shearing forces and get access to the vulnerable ventral parts. The genus *Armadillo* possesses a schisma at the hind corner of the first epimeron which continues as a groove to the frontal corner (Fig. 11) and even on the frontal part of the head (Fig. 12). In the rolled-up animal the margins of the 6th and 7th pereion-

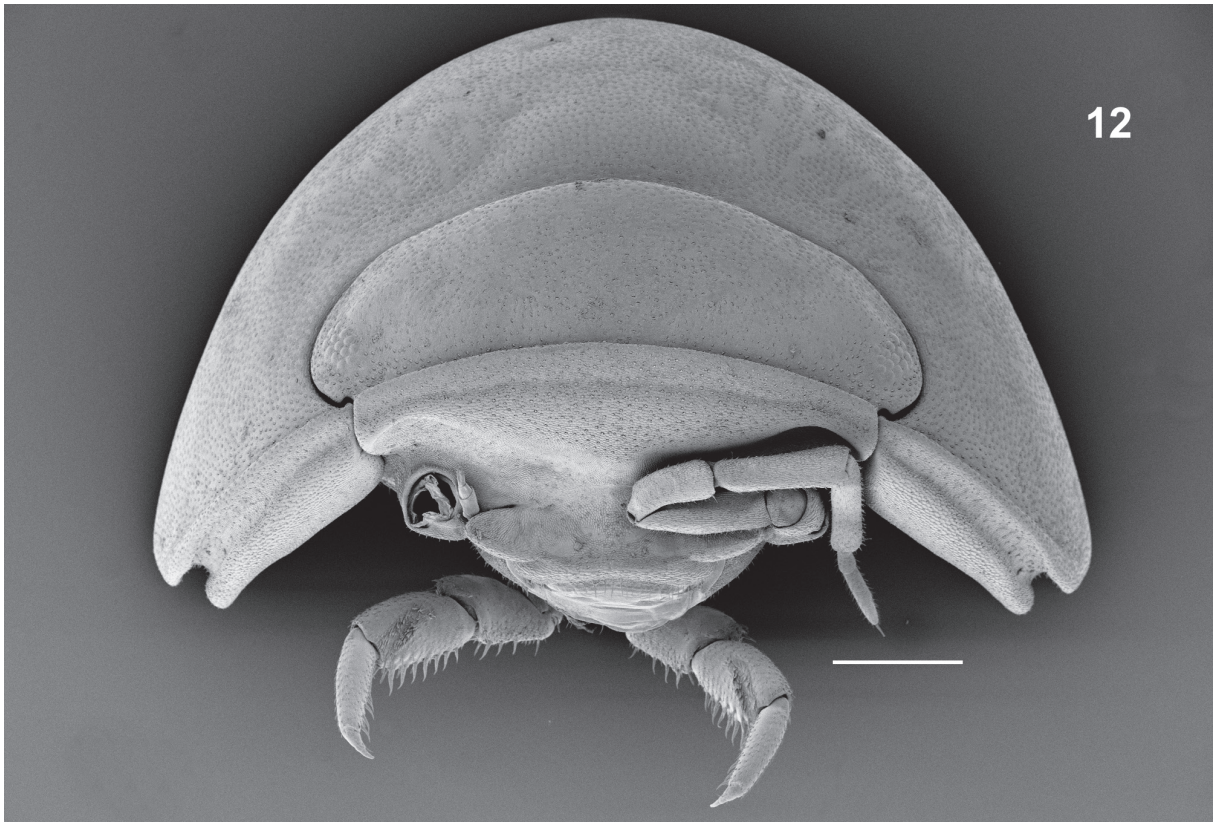


Fig. 12. *Armadillo officinalis*, frontal view of head and pereion-tergite 1. Note continuation of epimeral grooves on frontal part of head. – Scale: 1 mm.

tergites fit into this groove, so the animal is secured against shearing forces, and the posterior margins of the pleon-epimera and the telson are tightly pressed against the depression on the frontal margin of the head. In this way, as it is the case in *Schizidium*, the rolled-up animal does not offer any fissures for pointed appendages to get access to the vulnerable ventral parts.

The *Schizidium* species populate the eastern Mediterranean region and the Middle East countries north of the desert belt, where they live in open dry maquis and phrygana biotopes. Considering their morphological adaptations which have obviously been acquired to minimize predation, it seems that in these biotopes the crucial part of the predator spectrum consists of arthropods. This would mean selective advantages over competitors like *Armadillidium*, and it would explain the present-day distribution of *Schizidium*. On the other hand – contrasting the Greek mainland with the southern Aegean islands – other segments of the predator spectrum, e. g. mammals, should dominate in the continental biotopes with denser and higher vegetation. Shrews for instance, practically lacking on the islands, certainly could take a heavy toll on prey like isopods. In these biotopes – as far as the Greek region is concerned – *Armadillidium* is obviously the better adapted group of the conglobating isopods. The genus *Armadillo*, with morphological anti-predation strategies similar to those of *Schizidium*, is present with two species in the Aegean region (one only on the islands). In the Near East it penetrates into semi-desert and desert biotopes, where it has differentiated into a dozen different species (SCHMALFUSS 1996).

6 Conclusions

In the "rollers" among terrestrial isopods different types of morphological adaptations exist. The three genera *Armadillidium*, *Schizidium* and *Armadillo* are the dominating conglobating groups in the eastern Mediterranean region. Each of these genera exhibits a different set of characters to perform the rolling-up behavior. The different strategies obviously lead to different survival values in the biotopes prevailing in the treated region. *Armadillidium* seems to have advantages in continental biotopes with dense and highly developed vegetation, *Schizidium* is the dominant group in open dry maquis and phrygana

biotopes, and *Armadillo* has its highest species numbers and population densities under semi-desert conditions.

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