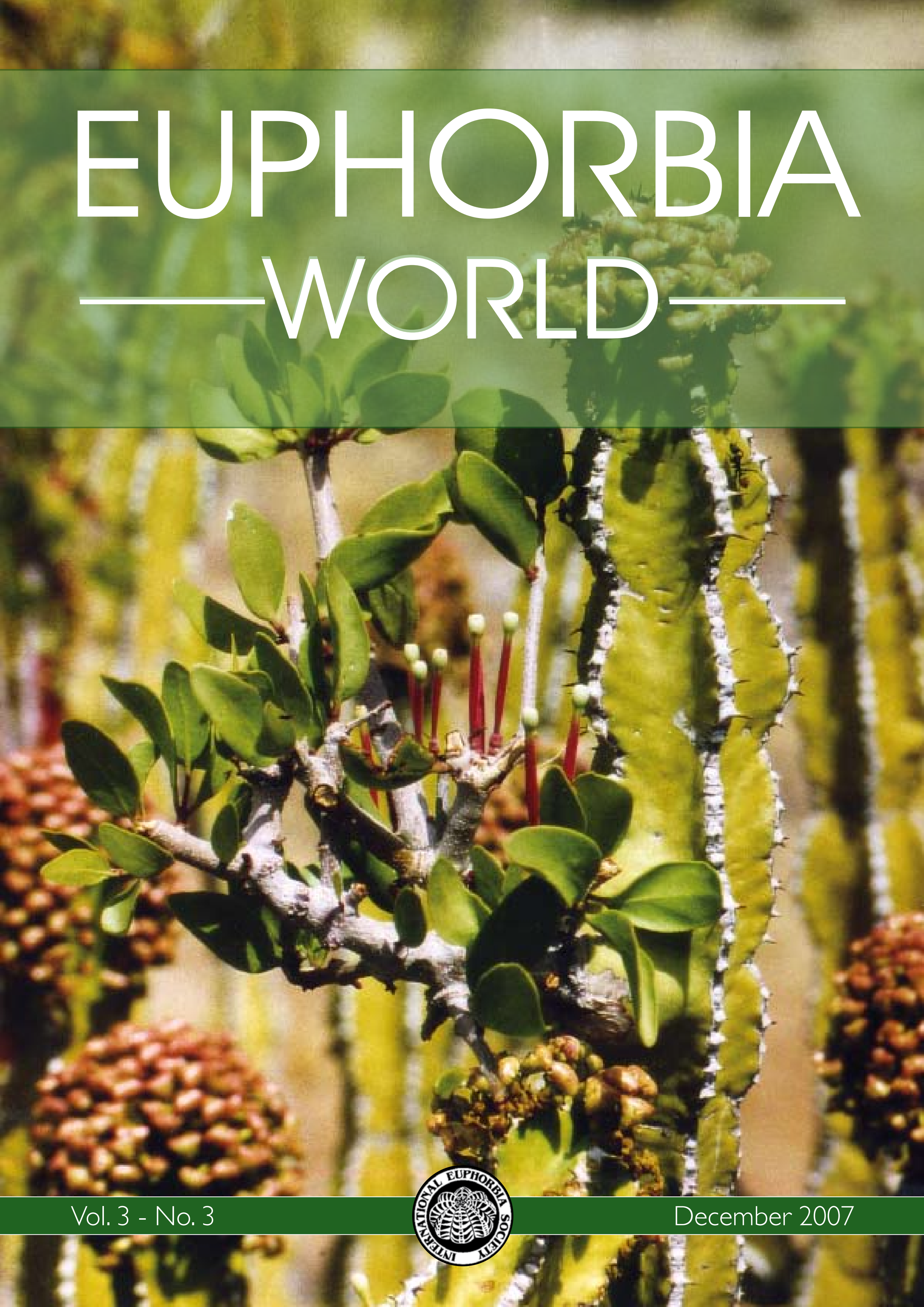

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Parasitic flowering plants on Euphorbia in South Africa and Namibia

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By definition parasitic plants get nutrients, carbohydrates, ions and water from their host plants (Weber 1993) and they develop special morphological features to survive on the living tissue of other plants. The haustorium connects the parasite with its host and allows the transportation of water, inorganic and organic compounds into the parasite. Holoparasites are unable to produce chlorophyll for photosynthesis and are totally dependent on their hosts. A second group are the semi-parasites; their leaves produce chlorophyll and they are able to photosynthesise.

From South Africa and Namibia 67 parasitic flowering plants are known, 23 are stem parasites and 44 are root parasites (Visser 1981). Mainly woody species are potential hosts for the parasites, but also succulents like *Aloe dichotoma, Cotyledon* and *Lampranthus* are listed as hosts (Visser 1981, Veste 2005). The highest diversity

Fig. 1: Hydnora africana *exposing the entrance of the flower above ground (Photo: Siegmar-W. Breckle).*

Fig. 2: Hydnora triceps *flower in Namaqualand. Most of the flower is subterranean and only excavated for the picture.*

of parasites growing on succulents can be found on *Euphorbia* species (table 1). Four root parasites and four mistletoes belonging to four families can be found on stem succulent *Euphorbia* species in South Africa and Namibia.

Root parasites

The most remarkable root parasites of Africa with a most "unplantlike" appearance belong to the Hydnoraceae. In Southern Africa only two species from this family occur: *Hydnora africana* and *Hydnora triceps* and both species are restricted to parasites on *Euphorbia* spe-

Fig. 3: The subterranean network of the haustorial "roots" of Hydnora triceps *parasitic on* Euphorbia dregeana. *The scale in the picture is 10 cm.*

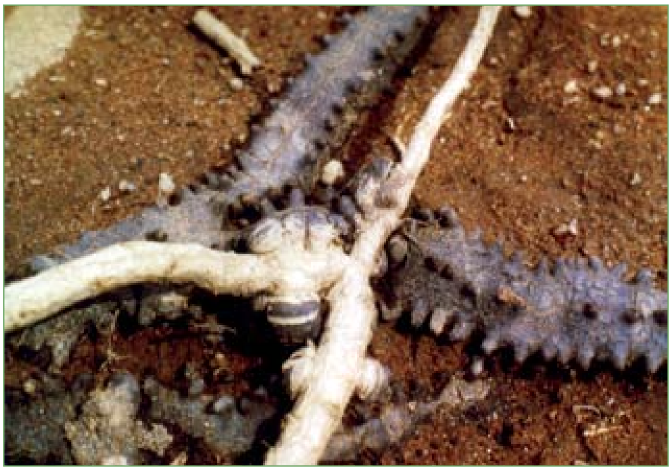

Fig. 4: Connection between Hydnora triceps *and the root of* Euphorbia dregeana.

cies. *Hydnora africana* (Fig. 1) has a wide distribution area from the Cape Peninsula northwards up the Nama Karoo in Namibia and eastwards to Eastern Cape.

The rarest root parasite is *Hydnora triceps* (Fig. 2). The botanist Johann F. Drège discovered this species near Okiep in Namaqualand in the 1830. The distribution is restricted to a small area of the Namaqualand and southern Namibia. Only a few specimens were collected and deposited in herbaria. For nearly 100 years this *Hydnora* species sank into oblivion until 1988, when Johann Visser, professor of botany at the University of Stellenbosch, rediscovered *H. triceps* in the sandveld of Namaqualand (Visser 1989). Until now only a few records were made of this rare plant. Only two years after the observation by Visser the author was able to visit this population in the sandveld south of the road between Springbok and Port Nolloth in the north-western part of Namaqualand. The area is characterized by succulent dwarf shrubs, mainly mesembs and *Euphorbia* species (Veste & Jürgens 2004). Meanwhile another population was discovered by Maass & Musselman (2004) near Rosh Pinah in southern Namibia. *Hydnora triceps* is restricted only to *Euphorbia dregeana*, even when other *Euphorbia* species grow nearby. *Euphorbia dregeana* is distributed in Namaqualand and southern Namibia. It is estimated that only 10 % of *E. dregeana* in the Port Nolloth area and less than 0.5 % in southern Namibia are parasitized by *H. triceps* (Maass & Musselman 2004).

The hidden way of life of the parasites makes it difficult to find this plant in the wild. Most parts of the plant consist of a subterranean network of fleshy so-called "pilot roots" connected to the root system of the hosts. Fig. 3 shows such a subterreanean network of *Hydnora triceps* connected to the roots of the nearby *Euphorbia dregeana*. The *Hydnora* haustorium is directly

Table 1: Parasitic flowering plants on Euphorbia *in South Africa and Namibia (after [1] Visser 1981, [2] Visser 1989, [3] Midgley et al. 1994, [4] own observation 1990/91). Note [1]: Visser (1981) mentions only the genus and not the species.*

Parasite	Family	Host	Reference
Root parasites:			
Alectra vogelii Benth.	Scrophulariaceae	*Euphorbia*[1]	[1]
Buttonia superba Oberm.	Scrophulariaceae	*Euphorbia*[1]	[1]
Hydnora africana Thunb.	Hydnoraceae	*Euphorbia*[1]	[1]
Hydnora triceps Drege	Hydnoraceae	*Euphorbia dregeana* E. Meyer ex Boissier	[2, 4]
Stem parasites:			
Tapinanthus oleifolius (J.C.Wendl.) Danser	Loranthaceae	*Euphorbia virosa* Willd.[1]	[1, 5]
Viscum capense L. f.	Viscaceae	*Euphorbia*[1]	[1]
Viscum crassulae Eckl. & Zeyh.	Viscaceae	*Euphorbia* species aff. *tetragona* *Euphorbia grandidens* Haw.	[1] [3]
Viscum minimum Harv.	Viscaceae	*Euphorbia polygona* Haw.	[1]

connected to the xylem and the phloem of the host's roots (Fig. 4). The structure of the pilot-roots bearing the flowers and the haustoria remains unclear (Visser 1981, Weber 1993). However, its anatomical structure shows characteristics for stems (Tennakoon et al 2005). From buds along this vegetative body the haustorium and the flowers are developed exogenously. It can take more than one year for the development of a flower. Only the entrance to the flowers is exposed above ground to attract pollinators (Fig. 1). The flowers of *Hydnora* are brown, warty or scaly on the outside and orange on the inside (Fig. 5). They have a putrid smell. Within one year the flower grows to a height of 10 to 15 cm (3.95 to 5.9 inches). Flowering time is from June to January. The fruits have a tough outer layer, which splits and exposes a pulpy mass in which the seeds are embedded. The fruits are eaten by small mammals and even by birds. The delicious fruits are part of the traditional food of the local Khoi in northern South Africa and used for several Cape dishes (van Wyk & Gerike 2000). The fruits have a sweet taste when baked on a fire.

Other root parasites growing on *Euphorbia* species are *Alectra vogelii* and *Buttonia superba* belonging to the Scrophulariaceae. *Buttonia* is a climber which rambles through shrubs often some distance from the hosts and occurs in the eastern provinces of South Africa.

Stem parasites

Xylem-tapping mistletoes are common in the arid and semi-arid regions of Southern Africa. The richest mistletoe flora can be found in the summer rainfall area of the Nama Karoo, where thirteen species occur (Dean et al. 1994). In the winter rainfall desert of the Succulent Karoo eight species can be found. The mistletoes are represented by the Viscaceae *Viscum* and the Loranthaceae *Moquiniella, Septulina* and *Tapinanthus* (Visser 1981). The host specificity varies between the different species. *Tapinanthus oleifolius* is not restricted to a specific host and it can be found on more than 30 hosts including *Acacia, Aloe, Citrus, Ficus, Rhus, Tamarix* and even other mistletoes like *Viscum* and *T. oleifolius* plants. *T. oleifolius* is the only Loranthaceae in Southern Africa growing on *Euphorbia virosa* (front cover). *Eu-*

Fig. 5: Cross-section of the flowers of (A) Hydnora africana, *left, (Photo: Siegmar-W. Breckle) and (B) of* Hydnora triceps, *above (Photo: Maik Veste).*

Fig. 6: Viscum minimum *parasitic on* Euphorbia horrida. *Only the small stem and 2-3 leaves and the inflorescence are visible (photo: S.-W. Breckle).*

phorbia virosa is up to 3 m (9.8 ft.) high and distributed from the area south of Vioolsdrift on the Orange River northwards to the Kaokoveld and southern Angola. A large population of *T. oleifolius* growing on *Euphorbia virosa* can be found in the Karas Mountains in southern Namibia, where the mistletoe is also growing on *Acacia nebrownii* and *Ziziphus mucronatha*. From Burkina Faso *Tapinanthus globiferus* and *T. ophiodes* growing on *Euphorbia balsamifera* are known (Boussim et al. 2004). *Viscum crassulae* is frequently found on *Euphorbia* spec. aff. *tetragona* and is also reported on *E. grandidens*.

The smallest mistletoe is *Viscum minimum* barely growing taller than a few millimetres and is hard to find. The visible part is composed of a small stem with a single internode of 0.5 mm (0.02 in.), 2 or 3 leaves and a single inflorescence (Fig. 6). Most of the plant consists of branching haustorium and is inside the host as an endoparasite. The distribution area ranges from the Little Karoo towards the Eastern Cape. Visser (1981) reported that *Viscum minimum* is parasitic almost exclusively on *Euphorbia polygona* and *E. horrida*. However, in an experiment it was possible to establish *V. minimum* successfully on 28 succulent *Euphorbia* species from the area south of the Sahara, Morocco and Madagascar (Heide-Jørgensen 2004).

Birds are important for the seed dispersal of all mistletoes. The berries are picked up by fruit-eating birds. The berries are ripe when food is rather scarce and a large variety of birds are attracted. They defecate the seeds of the Loranthaceae within minutes, while the *Viscum* seeds are retained slightly longer. Most of the seeds are distributed on the nearby plants up to 50 meters (164 ft.) from the fruiting plant (Visser 1981) and therefore, mistletoes are distributed in clumps in the landscape. Once the seed is removed from the fruit germination can start and the hypocotyls grow towards the branch. The penetration into the host's tissue and the essential contact with the xylem can take up to one year.

Ecophysiology of mistletoes

Even though *Tapinanthus oleifolius* is able to photosynthesise, the heterotrophic carbon gain from its host *Euphorbia* has been found to be 55 % in young leaves and more than 80 % in old succulent leaves (Richter et al. 1995). The daily CO_2 uptake of *Tapinanthus* was 96 mmol per m^2 leaf surface per day in young leaves and only 29 mmol per m^2 per 24 h in old leaves. However, daily transpiration of the mistletoe was 68 mol per m^2 per 24 h in young leaves and 239 mol per m^2 per 24 h in old leaves (von Willert & Popp 1995). This shows the importance of the influx of water, ions and organic components into the leaves of the parasite. The water supply of the xylem-tapping mistletoes by the host is an important feature for this association. A water potential gradient is essential for the water fluxes and the nutrient fluxes from the hosts to the mistletoe. In general, transpiration rate of the parasite is higher than its hosts, e.g. *Viscum crassulae* had a four times higher transpiration rate than its host *Euphorbia grandidens* (Midgley et al. 1994).

Typical for *Tapinanthus oleifolius* growing on *Euphorbia virosa* are its succulent leaves. Ions are transported by the transpiration stream in the parasite resulting in a high ion accumulation, especially of potassium and chloride (Fig. 7). Succulence shows a clear interrelation with the chloride content. Chloride induces the development of the leaf succulence of *Tapinanthus*. A similar increase of ion content and leaf succulence can be observed in mistletoes growing on halophytic hosts. When *Tapinanthus oleifolius* (Namibia) or *Psilocephalus* (syn. *Loranthus*) *acaciae* (Arava-Valley, Israel) were parasitic on halophytic *Tamarix* trees, water content and leaf volume increased significantly in old leaves in comparison to individuals growing on non-halophytic *Acacia* trees (Popp et al.

1995, Veste & Breckle 1995). The increase of succulence dilutes the ions and other organic osmolytes (sugars, organic acids, cyclitolts) in the cell and the osmotic concentration is even lower than on the non-halophytic host. As on other halophytes the increasing succulence is a morphological adaptation for the mistletoe to the increasing salt stress on halophytic hosts. ♦

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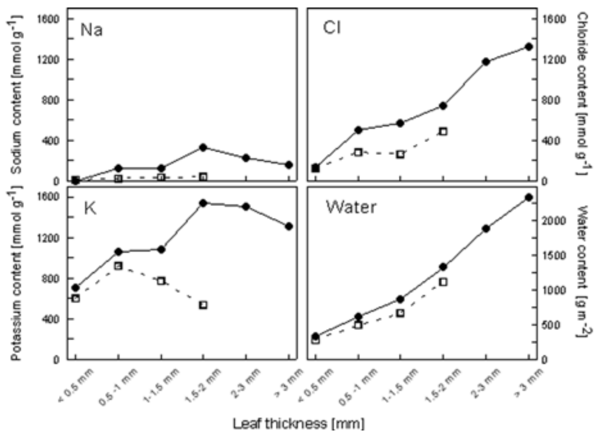

Fig. 7: Ion content [mmol per g dry weight] and water content [g per m² leaf surface] in leaves of Tapinanthus oleifolius *parasitizing on the succulent* Euphorbia virosa *(circles) and the non-succulent* Acacia karoo *(squares) in the Karas Mountains, Namibia (after Popp et al. 1995). (Note: Negative superscripts in the figure denote "per"; any amount of substance is given in molecules, symbol "mol"; mmol = millimol)*

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