Ribosome-Inactivating and Related Proteins

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Abstract: Ribosome-inactivating proteins (RIPs) are toxins that act as N-glycosidases (EC 3.2.2.22). They are mainly produced by plants and classified as type 1 RIPs and type 2 RIPs. There are also RIPs and RIP related proteins that cannot be grouped into the classical type 1 and type 2 RIPs because of their different sizes, structures or functions. In addition, there is still not a uniform nomenclature or classification existing for RIPs. In this review, we give the current status of all known plant RIPs and we make a suggestion about how to unify those RIPs and RIP related proteins that cannot be classified as type 1 or type 2 RIPs.

Keywords: ribosome-inactivating proteins; RIPs; type 1 RIP; RIP 1; type 2 RIP; RIP 2; N-glycosidase; nomenclature of RIPs; classification of RIPs

1. Introduction

Because of their N-glycosidase activity, ribosome-inactivating proteins inhibit protein synthesis by cleaving a specific adenine residue (A\textsuperscript{4324}) from the 28S ribosomal RNA of the large 60S subunit of rat ribosomes followed by cell death [1]. In addition, certain RIPs can remove adenine from DNA and other polynucleotides for which reason they are also known as polynucleotide adenosine glycosidases [2]. PAP, an RIP from Phytolacca americana, can cleave not only adenine, but also guanine from the rRNA of Escherichia coli [3].

There are mainly two different types of RIPs: type 1 RIPs (RIP 1) and type 2 RIPs (RIP 2). Type 1 RIPs are single chain proteins, whereas type 2 RIPs consist of two polypeptide chains (A- and B-chain)
that are usually linked through a disulfide bridge. The A-chain contains the enzymatic function and the B-chain has lectin properties enabling these proteins to bind to galactose residues on the cell surface. This facilitates the A-chain to enter the cell. Beside these different types of RIPs, there was the proposal to categorize an additional group of RIPs as type 3 RIPs including a protein from maize (b-32) and from barley (JIP60). The protein from maize, b-32, is synthesized as an inactive proenzyme, which is activated after the removal of an internal peptide segment obtaining two segments of 16.5 kDa and 8.5 kDa [4] that seem to act together as N-glycosidase. JIP60 consists of an amino-terminal domain resembling type 1 RIPs linked to a carboxyl-terminal domain, which has a similarity to eukaryotic translation initiation factor 4E [5,6]. Due to their different structures, these two proteins cannot be grouped into the classical type 1 RIPs. However, the necessity of denominating a new group of RIPs for only these two proteins is not realistic. Therefore, the suggestion was made to consider these two proteins as peculiar type 1 RIPs [7,8]. Beside the N-glycosidases, there is a second kind of RIPs belonging to the RNA hydrolase [9,10]. Both kinds of RIPs strongly inhibit the protein synthesis but show different mechanisms of action. The RNA hydrolases, like α-sarcin as the best-known representative, catalytically cleave a phosphodiester bond between G[4325] and A[4326] of the rat 28S rRNA. With the exception of crotin II, another representative of the RNA hydrolases (see Section 3.5), these kinds of RIPs are not described in detail in this review.

RIPs have mostly been found in plants, but the hypothesis that RIPs are ubiquitous should be discarded, because a gene encoding for an RIP has not been detected in the genome of Arabidopsis thaliana [11]. On the other hand, there are plants in which several RIPs occur simultaneously, and recently, it was shown that there are 31 genes in the rice genome encoding for type 1 RIPs [12]. Beside the plant RIPs, a type 1 RIP was also found from the species algae Saccharina japonica, which were denominated as lamjapain [13]. In addition, researchers are also aware of some type 1 RIPs from fungi, such as pleuuregin from Pleurotus tuberregium [14], lyophyllin from Lyophyllum shimeji [15], flammatin and velutin from Flammulina velutipes [16], hyspin and marmorin from Hypsizygus marmoreus [17,18], and volvarin from Volvariella volvacea [19]. There are also two type 1 RIPs from bacteria: shiga toxin from Shigella dysenteria [20], and verotoxin 1 (shiga-like toxin) from Escherichia coli [21]. At last, adenine glycosylase activity was even found in some mammalian tissues [2].

RIPs show several enzymatic activities, such as chitinase activity [22], superoxide dismutase activity [23], DNase activity [24], and lipase activity [25]. Due to the N-glycosidase activity on viral RNA, RIPs have an antiviral effect, which is considered as a physiological function. But the enzymatic activity could also be related to a role in the defense of plants against predators and fungi [7,8,26]. Because of the N-glycosidase activity on genomic plant DNA, it is also believed that RIPs could play an undefined role in plant senescence [27]. RIPs might also give the plants evolutionary advantages as a kind of protection under unfavorable situations [28]. Anyway, no precise biological role has yet been assigned to RIPs [29], but most of the authors favor the antiviral role. Thus, in agriculture, research was performed to increase the resistance against viruses by using DNA recombinant technology (reviewed in [11]). In medicine, research for treatment of HIV diseases was performed leading to phase II study [30]. But most research of the use of RIPs is aimed at anti-cancer therapy in leading RIPs selectively to malignant tumor cells to be eliminated. Therefore, type 1 RIPs and the A-chains of type 2 RIPs are coupled to antibodies or other targeting moieties like growth factors, other hormones or smaller peptides
generating targeted toxins [31–33]. These conjugates, however, contain highly potent toxins with a high potential of side effects, because they are partly taken up non-specifically by macrophages or other somatic cells. Another issue regarding the application of these conjugates in an anti-cancer therapy is the response of the immune system, because they are antigens. To reduce at least the high potential of side effects, it is necessary to begin the dosage of these conjugates as low as possible. That seemed to be possible since a synergistic effect of saponins and type 1 RIPs increasing the toxic effect of type 1 RIPs drastically [34–36] has been discovered. For that, the saponins must consist of certain molecule units [37], and it has been found that the synergistic effect is not based on stimulating phagocytosis [38], but increasing the endosomal escape in a certain way [39,40]; thus, the type 1 RIPs enter the cytosol.

In the last decade, several reviews about RIPs were published setting the focus on the chemical and biological properties and activities, distribution in nature or possible use of the RIPs (e.g., [8,11,41–44]). There is one review that contains a table of all hitherto known RIPs [7]. During our investigations, we found that this table needs to be added with several more RIPs and RIP related proteins. Moreover, we found that some proteins were designated with different terms, e.g., nigrin b from Sambucus nigra or sieboldin-b from Sambucus sieboldiana were also designated as SNA-V or SSA-b-2, respectively. In addition, in some cases, the same term was used to designate different proteins, e.g., the term momordin II was used for a protein from Momordica balsamina as well as for a protein from Momordica charantia or the term MAP was used for a protein (MAP 30) from Momorica charantia and for a protein from Mirabilis jalapa (MAP = Mirabilis antiviral protein). These examples are intended to illustrate that there is still no unambiguous nomenclature for the RIPs. There are also ambiguities about the classification of some proteins, whether they are type 2 RIPs or just lectins, because no assay concerning the toxicity was performed or there was no information given about the structure: SGSL from Trichosanthes anguina, TCSL from Trichosanthes cucumerina, TKL-1 from Trichosanthes kirilowii, TDSL from Tichosanthes dioica, and BDA from Bryonia dioica. At least since the knowledge that RIPs and lectins evolved from common ancestral genes [29], it is very likely that there are a number of other RIPs not detected to date. This assumption is corroborated by the investigation of several Adenia species, in which some new lectins were found, some of which may be referred to as type 2 RIP [45]. Therefore, with this review we created a summary table (Table 1) with all known RIPs and those proteins, which probably can be classified as RIPs, and we listed all terms that were used for the designation of these proteins. Since there is a phylogenetic relationship between RIPs and lectins, as mentioned above, we also listed the lectins from those plants, which are members of families that are known to include plants that synthesize one or more RIPs. For this, we focused on RIPs from plants, whereas other RIPs from algae, bacteria, and fungi are not considered further.
2. Table of RIPs from plants

Table 1. Summary table of ribosome-inactivating proteins (RIPs) and RIP related proteins from plants.

| Family       | Species 1 | Protein     | Classification | MW 2 | IC50 3 | Source | References |
|--------------|-----------|-------------|----------------|------|--------|--------|------------|
| **Sambucus ebulus L.** |           | Ebutilin α  | RIP 1           | 32 kDa | 10 ng/mL | leaves | [46]       |
|              |           | Ebutilin β  | RIP 1           | 29 kDa | 10 ng/mL | leaves | [46]       |
|              |           | Ebutilin γ  | RIP 1           | 29 kDa | 10 ng/mL | leaves | [46]       |
|              |           | Ebutilin f  | RIP 2           | 56 kDa | 96 ng/mL; 0.3 nM (A) 4 | green fruits | [29,47] |
|              |           | Ebutilin l  | RIP 2           | 56 kDa | 8.5 ng/mL; 0.15 nM (A) 5 | leaves | [29,48,49] |
|              |           | Ebulin r1   | RIP 2           | 56 kDa | 2.3 ng/mL | rhizomes | [49]       |
|              |           | Ebulin r2   | RIP 2           | 56 kDa | 2.3 ng/mL | rhizomes | [49]       |
|              |           | SEA         | RIP 2           | 135,630 Da | 1 nM | leaves | [50]       |
|              |           | SEAII       | lectin          | 33.5 kDa | - | rhizomes | [49]       |
|              |           | SELfd       | lectin          | 68 kDa | 820 ng/mL | green fruits | [47] |
|              |           | SELld       | lectin          | 67,906 Da | - | leaves | [51,52] |
|              |           | SELlm       | lectin          | 34,239 Da | - | young shoots | [53] |
|              |           | α-Nigritin  | RIP 1           | 29 kDa | 2.44–34 ng/mL | leaves | [54]       |
|              |           | β-Nigritin  | RIP 1           | 40 kDa | 2.44–34 ng/mL | leaves | [54]       |
|              |           | γ-Nigritin  | RIP 1           | 27.5 kDa | 2.44–34 ng/mL | leaves | [54]       |
|              |           | Nigrin fl   | RIP 1           | 24,095 Da | 100 ng/mL | green and mature fruits | [55] |
|              |           | Nigrin f2   | RIP 1           | 23,565 Da | 100 ng/mL | mature fruits | [55] |
|              |           | basic Nigrin b | RIP 2     | 63,469 Da | 18 pg/mL; 0.3 pM (A) 4 | bark | [56] |
|              |           | Nigrin b = SNA-V | RIP 2   | 120 kDa | 261 pM; 0.03 nM (A) 5 | bark | [29,57–59] |
|              |           | Nigrin f = SNA-VI | RIP 2 | 120 kDa | 1.9 ng/mL; 1.8 ng/mL; 0.03 nM (A) 5 | fruits | [29,60–62] |
|              |           | Nigrin l1   | RIP 2           | n.a. 4 | n.a. 4 | leaves | [63]       |
|              |           | Nigrin l2   | RIP 2           | n.a. 4 | n.a. 4 | leaves | [63]       |
|              |           | Nigrin s    | RIP 2           | 57 kDa | ~1 µg/mL | seeds | [64]       |
|              |           | SNA-I       | RIP 2           | 240 kDa | 150 ng/mL; 600 pM | bark | [58,65–68] |
|              |           | SNA-I’      | RIP 2           | 120 kDa | 150 ng/mL | bark | [67,69] |
|              |           | SNA-lf      | RIP 2           | 240 kDa | n.a. 4 | fruits | [69,70] |
|              |           | SNAflu-I subunits of | RIP 2 | 30–33 kDa | n.a. 4 | inflorescences | [71,72] |

1. Sambucus nigra L.
| Family                  | Species 1 | Protein | Classif. | Mw 2 | IC₅₀ 3 | Source | References |
|------------------------|-----------|---------|----------|------|--------|--------|------------|
| **Adoxaceae**          |           |         |          |      |        |        |            |
| *Sambucus nigra* L.   |           |         |          |      |        |        |            |
| SNLRP1                 | RIP 2     | 62 kDa  | 0.5 µg/mL; 5.74 nM (A) 4 | bark | [29,73,74] |
| SNLRP2                 | RIP 2     | 60–62 kDa | n.a. 4 | bark | [74]   |
| SNA-ld                 | lectin    | n.a. 4  | -        | leaves | [63]  |
| SNA-im                 | lectin    | n.a. 4  | -        | leaves | [63]  |
| SNA-II                 | lectin    | 60 kDa  | -        | bark | [58,68,75] |
| SNA-III                | lectin    | 50 kDa  | -        | seeds | [58,76] |
| SNA-IV = SNA-IVf       | lectin    | 60 kDa  | -        | fruits | [58,62,77,78] |
| SNA-IVI                | lectin    | n.a. 4  | -        | leaves | [63]  |
| SNAPol-I               | lectin    | subunits of 26 kDa | - | pollen | [71] |
| SNApol-II              | lectin    | subunits of 20 kDa | - | pollen | [71] |
| TrSNA-I                | lectin    | 22 kDa  | -        | bark | [70]   |
| TrSNA-If               | lectin    | 22 kDa  | -        | fruits | [70]  |
| **Aizoaceae**          |           |         |          |      |        |        |            |
| *Sambucus racemosa* L. |           |         |          |      |        |        |            |
| basic racemosin b      | RIP 2     | n.a. 4  | n.a. 4   | bark | [72]   |
| SRA                    | RIP 2     | 120 kDa | n.a. 4   | bark | [72,79] |
| SRLbm = SRAbm          | lectin    | 30 kDa  | -        | bark | [72,80] |
| **Aizoaceae**          |           |         |          |      |        |        |            |
| *Mesembryanthemum*     |           |         |          |      |        |        |            |
| *crystallinum*         | L.        |         |          |      |        |        |            |
| RPI                   | RIP 1     | 31.6 kDa | n.a. 4   | leaves | [85]  |
| **Amaranthaceae**      |           |         |          |      |        |        |            |
| *Amaranthus*           |           |         |          |      |        |        |            |
| *caudatus* L.          |           |         |          |      |        |        |            |
| Amaranthin = ACA       | lectin    | 63.5 kDa | -        | seeds | [86–88] |
| *Amaranthus*           |           |         |          |      |        |        |            |
| *cruentus* L.          |           |         |          |      |        |        |            |
| ACL                   | lectin    | 66 kDa  | -        | seeds | [89]   |
| *Amaranthus*           |           |         |          |      |        |        |            |
| *hypochondriacus* L.   |           |         |          |      |        |        |            |
| [Syn.: *Amaranthus*     |           |         |          |      |        |        |            |
| *leucocarpus*          | lectin    | 45 kDa  | -        | seeds | [90]   |
| *S. Watson*]           |           |         |          |      |        |        |            |
| *Amaranthus*           |           |         |          |      |        |        |            |
| *mangostanus* L.       |           |         |          |      |        |        |            |
| Amaramangin            | RIP 1     | 29 kDa  | n.a. 4   | seeds | [91]   |
| *Amaranthus*           |           |         |          |      |        |        |            |
| *tricolor* L.          |           |         |          |      |        |        |            |
| AAP-27                 | RIP 1     | 27 kDa  | n.a. 4   | leaves | [92]  |

Notes:
1. Species 1: The species name is the first of the two species names listed in the table.
2. Mw: Molecular weight.
3. IC₅₀: Inhibitory concentration 50%.
4. n.a.: Not available.
5. A: Activity.

References:
[29,73,74] [74] [63] [58,68,75] [58,62,77,78] [71] [72] [81–83] [86–88] [89] [90] [91] [92]
Table 1. Cont.

| Family          | Species ¹                                      | Protein         | Classific. | Mw ² | IC₅₀ ³ | Source            | References     |
|-----------------|------------------------------------------------|-----------------|------------|------|--------|-------------------|----------------|
| Amaranthaceae   | *Amaranthus viridis* L.                         | Amaranthin      | RIP 1      | 30 kDa | 25 pM  | leaves            | [93,94]        |
|                 | *Beta vulgaris* L.                              | Beetin-27 = BE27| RIP 1      | 27,592 Da | 1.15 ng/mL | leaves | [95–97]        |
|                 |                                                 | Beetin-29 = BE29| RIP 1      | 29 kDa   | n.a.   | leaves            | [95–97]        |
|                 |                                                 | Betavulgin      | RIP 1      | 30 kDa   | n.a.   | seedlings         | [98]           |
|                 | *Celosia argentea* L. [Syn.: *Celosia cristata* L.] | CCP-25          | RIP 1      | 25 kDa   | n.a.   | leaves            | [99,100]       |
|                 |                                                 | CCP-27          | RIP 1      | 27 kDa   | 25 ng/mL | leaves            | [99–101]       |
| Chenopodium     | *album* L.                                      | CAP30           | RIP 1      | 30 kDa   | 2.26 pM | leaves            | [102,103]      |
| Spinacia        | *oleracea* L.                                   | SoRIP1 = BP31   | RIP 1      | 31 kDa   | n.a.   | cell cultures     | [104–107]      |
|                 |                                                 | SoRIP2          | RIP 1      | 36 kDa   | n.a.   | cell cultures     | [106,107]      |
| Araliaeae       | *Aralia elata* (Miq.) Seem.                     | Aralin          | RIP 2      | 62 kDa   | n.a.   | shoots            | [108,109]      |
|                 | *Panax ginseng* C.A.Mey                         | Panaxagin       | peculiar   |          | 0.28 nM | roots             | [110]          |
|                 |                                                 | Panaxagin       | RIP 1 candidate/ RNase | 52 kDa |          |                   |                |
|                 | *Panax quinquefolius* L.                        | Quinqueginsin   | peculiar   |          | 0.26 nM | roots             | [111]          |
|                 |                                                 | Quinqueginsin   | RIP 1 candidate/ RNase | 53 kDa |          |                   |                |
| Asparagaceae    | *Asparagus officinalis* L.                      | Asparin 1       | RIP 1      | 30.5 kDa | 0.27 nM | seeds             | [112,113]      |
|                 |                                                 | Asparin 2       | RIP 1      | 29.8 kDa | 0.15 nM | seeds             | [112,113]      |
|                 | *Drimia maritima* (L.) Stearn [Syn.: *Charybdis maritima* (L.) Speta] | Charybdin      | RIP 1      | 29 kDa   | 27.2 nM | bulbs             | [114]          |
|                 | *Muscari armeniacum* Leichtlin ex Baker        | Musarmin 1      | RIP 1      | 28,708 Da | 7 ng/mL | bulbs             | [115]          |
|                 |                                                 | Musarmin 2      | RIP 1      | 30,003 Da | 9.5 ng/mL | bulbs             | [115]          |
|                 |                                                 | Musarmin 3      | RIP 1      | 27,626 Da | 4 ng/mL  | bulbs             | [115]          |
|                 |                                                 | Musarmin 4      | RIP 1      | 28 kDa   | 1.4–8.2 ng/mL; 50–280 nM | recomb. ⁶ | [116]          |
|                 | *Polygonatum multiflorum* (L.) All.             | PMRIPm          | RIP 2      | 60 kDa   | n.a.   | leaves            | [117]          |
|                 |                                                 | PMRIPt          | RIP 2      | 240 kDa  | n.a.   | leaves            | [117]          |
|                 | *Yucca gloriosa* var. *tristis* Carrière [Syn.: *Yucca recurvifolia* Salisb.] | Yucca leaf protein = YLP | RIP 1      | 23 kDa   | n.a.   | leaves            | [118,119]      |
| Basellaceae     | *Basella rubra* L.                              | Basella RIP 2a  | RIP 1      | 30.6 kDa | 1.70 ng/mL | seeds             | [120]          |
|                 |                                                 | Basella RIP 2b  | RIP 1      | 31.2 kDa | 1.70 ng/mL | seeds             | [120]          |
|                 |                                                 | Basella RIP 3   | RIP 1      | 31.2 kDa | 1.66 ng/mL | seeds             | [120]          |
| Family                | Species 1 | Protein         | Classific. | Mw 2  | IC₅₀ 3 | Source | References |
|-----------------------|-----------|-----------------|------------|-------|-------|--------|------------|
| Agrostemma githago L. | Agrostin 2| RIP 1           |            | 30.6 kDa | 0.6 nM | seeds | [121,122] |
|                       | Agrostin 5| RIP 1           |            | 29.5 kDa | 0.47 nM | seeds | [121,122] |
|                       | Agrostin 6| RIP 1           |            | 29.6 kDa | 0.57 nM | seeds | [121,122] |
|                       | Agrostin  | RIP 1           |            | 27 kDa   | n.a. 4 | seeds | [121,122] |
| Dianthus barbatus L.  | Dianthin 29| RIP 1           |            | 29 kDa   | 1.5 nM | leaves| [124]     |
| Dianthus caryophyllus L. | Dianthin 30| RIP 1          |            | 29.5 kDa | 9.15 ng/mL; 0.3 nM | leaves | [122,125,126] |
|                       | Dianthin 32| RIP 1          |            | 31.7 kDa | 3.6 ng/mL; 0.12 nM | leaves | [125,126] |
| Dianthus chinensis L. [Syn.: Dianthus sinensis Link] | D. sinensis RIP | RIP 1 | n.a. 4 | n.a. 4 | recomb. 6 | [127] |
| Gypsophila elegans M.Bieb. | Gypsophilin| RIP 1          |            | 28 kDa   | n.a. 4 | leaves| [128]     |
| Silene chalcedonica (L.) E.H.L.Krause [Syn.: Lychnis chalcedonica L.] | Lychnin | RIP 1 | 26,131 Da | 0.17 nM | seeds | [113,129,130] |
| Caryophyllaceae       | Silene glaucifolia Lag. [Syn.: Petrocoptis glaucifolia (Lag.) Boiss.] | Petroglucin 1 | RIP 1 | 26.7 kDa | 6 ng/mL | whole plants | [131] |
|                       |           | Petroglucin 2 | RIP 1 | 27.5 kDa | 0.7 ng/mL | whole plants | [132] |
|                       | Silene laxipruinosa Mayol & Rosselló [Syn.: Petrocoptis grandiflora Rothm.] | Petrograndin | RIP 1 | 28.6 kDa | 6.6 ng/mL | whole plants | [131] |
|                       | Saponaria ocyoides L. | Ocymoidin | RIP 1 | 30.2 kDa | 46 pM; 4.8 ng/mL | seeds | [133,134] |
|                       | Saporin-L1 = SO-L1 | R1 | 31.6 kDa | 0.25 nM | leaves | [135–138] |
|                       | Saporin-L2 = SO-L2 | R1 | 31.6 kDa | 0.54 nM | leaves | [135] |
|                       | Saporin-L3 = SO-L3 | R1 | n.a. 4 | n.a. 4 | leaves | [135] |
|                       | Saporin-1 = SO-1 = SO-4 | R1 | n.a. 4 | n.a. 4 | leaves | [135] |
|                       | Saporin-R1 = SO-R1 | R1 | 30.2 kDa | 0.86 nM | roots | [135] |
|                       | Saporin-R2 = SO-R2 | R1 | 30.9 kDa | 0.47 nM | roots | [135] |
| Family         | Species                                | Protein         | Classific. | Mw  | IC$_{50}$ | Source | References                  |
|---------------|----------------------------------------|-----------------|------------|-----|----------|--------|-----------------------------|
| Caryophyllaceae | Saponaria officinalis L.               | Saporin-R3  =  SO-R3 | R1         | 30.9 kDa | 0.48 nM | roots | [135]                        |
|               |                                        | SO3a           | R1         | 22.5 kDa | n.a.  | seeds | [140]                        |
|               |                                        | SO3b           | R1         | 19.4 kDa | n.a.  | seeds | [140]                        |
|               | Saporin-S5  =  Saporin 5  =  SO-S5     | R1             | 30.5 kDa | 0.05 nM; 10.3 ng/mL | seeds | [112,135,141]               |
|               | Saporin-S6  =  Saporin 6  =  SO-6  =  SO-S6 | R1       | 28,577 Da | 0.06 nM; 0.6 ng/mL | seeds | [112,135,139,141–145]       |
|               | Saporin-S8  =  SO-S8                   | R1             | n.a.      | n.a.  | seeds | [135]                        |
|               | Saporin-S9  =  Saporin 9  =  SO-S9     | R1             | 28,495 Da | 0.037 nM | seeds | [112,122,135,146]           |
|               | SAP-C                                  | R1             | 28.5 kDa | 125 pM | recomb. | [147]               |
|               | SAP-S                                  | R1             | 28,560 Da | 12 pM | seeds | [147]                      |
|               | Myosoton aquaticum (L.) Moench [Syn.: Stellaria aquatica (L.) Scop.] | Stellarin | R1 | 25 kDa | 0.04 nM | leaves | [148] |
|               | Stellaria media (L.) Vill.             | RIP Q3         | R1         | 28.2 kDa | n.a.  | recomb. 6  | [149] |
|               | Vaccaria hispanica (Mill.) Rauschert [Syn.: Vaccaria pyramidata Medik.] | Pyramidatin | R1 | 28.0 kDa | 89 pM; 3.6 ng/mL | seeds | [133] |
| Cucurbitaceae | Benincasa hispida (Thunb.) Cogn.       | Hispin         | R1         | 21 kDa | 165 pM | seeds | [150]               |
|               |                                        | α-benincasin   | sR1        | 12 kDa | 20 pM; 0.22 ng/mL | seeds | [151]             |
|               |                                        | β-benincasin   | sR1        | 12 kDa | 320 pM; 3.4 ng/mL | seeds | [151]               |
|               | Bryonia cretica subsp. dioica (Jacq.) Tutin. [Syn.: Bryonia dioica L.] | Bryodin 1 = BD1 | R1 | 29 kDa | 0.12 nM; 3.6 ng/mL; 7 pM | roots | [152,153] |
|               |                                        | Bryodin 2      | R1         | 27 kDa | 9 pM | roots | [153]               |
|               |                                        | Bryodin-L      | R1         | 28.8 kDa | 0.09 nM | leaves | [113] |
|               |                                        | Bryodin-R      | R1         | n.a.  | n.a.  | seeds | [154,155] |
|               |                                        | BDA           | lectin/ RIP 2 like | 61 kDa | >1500 nm | roots | [73,156] |

Table 1. Cont.

(n.a.) not available
Table 1. Cont.

| Family                  | Species ¹                  | Protein | Classific. | Mw ²       | IC₅₀ ³     | Source | References |
|-------------------------|---------------------------|---------|------------|------------|------------|--------|------------|
| Cucurbitaceae           | Cucurbita                  | Boxed   |            |            |            |        |            |
|                         | moschata                  | Duchesne |            |            |            |        |            |
|                         | [Syn.: Cucurbita           | moschata |            |            |            |        |            |
|                         | (Duchesne ex Lam.)         | Duchesne |            |            |            |        |            |
|                         | moschata                  | Duchesne |            |            |            |        |            |
|                         | [Syn.: Cucurbita           | texana   |            |            |            |        |            |
|                         | texana                    | (Scheele) |              |           |            |        |            |
|                         | [Syn.: Cucurbita           | texana   |      ²      |            |            |        |            |
|                         | texana                    | (Scheele) |              |           |            |        |            |
|                         | pepo                      | L.       |            |            |            |        |            |
|                         | var. texana               | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
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|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
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|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
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|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
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|                         | pepo                      | (Scheele) |            |            |            |        |            |
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|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
|                         | pepo                      | (Scheele) |            |            |            |        |            |
Table 1. Cont.

| Family      | Species ¹ | Protein     | Classif. | Mw ² | IC₅₀ ³ | Source | References |
|-------------|-----------|-------------|----------|------|-------|--------|------------|
| Luffa cylindrica (L.) M.Roem [Syn.: Luffa aegyptiaca Mill.] | Luffa cylindrica (L.) M.Roem [Syn.: Luffa aegyptiaca Mill.] | Luffin | RIP 1 | 26 kDa | 0.42 ng/mL | seeds | [176]     |
|             |           | Luffin-a    | RIP 1    | 27,021 Da | 1.64 ng/mL | seeds | [177,178] |
|             |           | Luffin-b    | RIP 1    | 27,275 Da | 0.84 ng/mL | seeds | [177,178] |
|             |           | α-luffin    | RIP 1    | 28 kDa | 10 ng/mL; 34.1 pM (recomb. ⁴) | seeds | [179–181] |
|             |           | β-luffin    | RIP 1    | 29 kDa | 50 ng/mL | seeds | [180,182] |
|             |           | LRIP        | RIP 1    | 30 kDa | 8 pM | seeds | [183]     |
|             |           | Luffacyclin | sRIP 1   | 7.8 kDa | 0.14 nM | seeds | [184]     |
|             |           | Luffin P1   | sRIP 1   | 5226.1 Da | 0.88 nM | seeds | [185]     |
|             |           | Luffin-S    | sRIP 1 candidate | 10 kDa | 0.34 nM | seeds | [186]     |
|             |           | LuffinS(1)  | sRIP 1 candidate | 8 kDa | 130 nM | seeds | [187]     |
|             |           | LuffinS(2)  | sRIP 1 candidate | 7.8 kDa | 10 nM | seeds | [187,188] |
|             |           | LuffinS(3)  | sRIP 1 candidate | 8 kDa | 630 nM | seeds | [187]     |
| Marah oreganus (Torr. & A. Gray) Howell | Marah oreganus (Torr. & A. Gray) Howell | MOR-I | RIP 1 | 27,989 Da | 0.063 nM | seeds | [189]     |
|             |           | MOR-II      | RIP 1    | 27,632 Da | 0.071 nM | seeds | [189]     |
| Cucurbitaceae | Momordica balsamina L. | Balsamin  | RIP 1    | 28.6 kDa | 90.6 ng/mL | seeds | [190]     |
|             |           | MbRIP-1     | RIP 1    | 30 kDa | n.a. ⁴ | seeds | [191,192] |
|             |           | Momordin II | RIP 1    | n.a. ⁴ | n.a. ⁴ | recomb. ⁶ | [193]     |
|             |           | MAP 30      | RIP 1    | 30 kDa | 3.3 nM | seeds | [194,195] |
|             |           | α-momorcharin | = α-MC = α-MMC | RIP 1 | 28,625–28,795 Da | 0.23 nM | seeds | [196–204] |
|             |           | β-momorcharin | = β-MC = β-MMC | RIP 1 | 29,074–29,076 Da | 0.19 nM | seeds | [196–198, 200–203] |
|             |           | γ-momorcharin | = γ-MMC | sRIP 1 | 11.5 kDa | 55 nM | seeds | [205]     |
|             |           | δ-momorcharin | = δ-MMC | RIP 1 | 30 kDa | 0.15 nM | seeds | [203]     |
|             |           | ε-momorcharin | RIP 1 candidate | 24 kDa | 170 nM | fruits | [203]     |
|             |           | Momordin    | RIP 1    | 31 kDa | n.a. ⁴ | seeds | [206]     |
|             |           | Momordin    | RIP 1    | 31 kDa | n.a. ⁴ | seeds | [207–212] |
|             |           | Momordin    | RIP 1    | n.a. ⁴ | n.a. ⁴ | seeds | [213]     |
Table 1. Cont.

| Family          | Species 1                                    | Protein        | Classific. | Mw 2 | IC₅₀ 3 | Source     | References               |
|-----------------|----------------------------------------------|----------------|------------|------|--------|------------|--------------------------|
| Cucurbitaceae   | Momordica charantia L.                       | Momordin-a     | RIP 1      | 29.4 kDa | n.a. 4 | seeds   | [214,215]               |
|                 |                                              | Momordin-b     | RIP 1      | 29.4 kDa | n.a. 4 | seeds   | [214]                   |
|                 |                                              | Charantin      | sRIP 1     | 9.7 kDa  | 400 nM | seeds   | [216]                   |
|                 |                                              | MCL            | lectin     | 12.4 kDa | -      | seeds   | [217]                   |
|                 | Momordica charantia L.                       | MCL = M. charantia lectin | R2  | 115–124 kDa | 1.74 µg/mL; 5 µg/mL | seeds | [207,218–220]|
|                 |                                              | MCL = Momordica charantia seed lectin | R2  | 115–124 kDa | 1.74 µg/mL; 5 µg/mL | seeds | [207,218–220]|
|                 |                                              | MCL = Momordica charantia lectin | R2  | 115–124 kDa | 1.74 µg/mL; 5 µg/mL | seeds | [207,218–220]|
|                 |                                              | MCL1           | lectin     | 150 kDa  | -      | seeds   | [221]                   |
|                 |                                              | anti-H Lectin  | lectin     | 30 kDa   | -      | seeds   | [222]                   |
|                 |                                              | Momordinagglutinin | lectin  | 49 kDa   | -      | seeds   | [223]                   |
|                 |                                              | protein fraction1 | lectin  | 49 kDa   | -      | seeds   | [224]                   |
|                 |                                              | protein fraction2 | lectin  | 49 kDa   | -      | seeds   | [224]                   |
|                 | Cochinin B                                   | RIP 1          | 28 kDa     | 0.36 nM  | seeds   | [225]               |
|                 | Momorcochin                                  | RIP 1          | 32 kDa     | n.a. 4   | tubers  | [200,226]             |
|                 | Momorcochin-S                                | RIP 1          | 30 kDa     | 0.12 nM  | seeds   | [225,227]             |
|                 | Siraitia grosvenorii (Swingle)               | Cochinin B     | RIP 1      | 28 kDa   | 0.36 nM | seeds   | [225]                   |
|                 |                                              | Momorgrosvin   | RIP 1      | 27.7 kDa | 0.3 nM  | seeds   | [228]                   |
|                 | Sechium edule (Jacq.) Sw.                    | Sechiumin      | RIP 1      | 27 kDa   | 0.1 nM  | seeds   | [229]                   |
|                 | Sechium edule fruit lectin                   | Sechiumin      | RIP 1      | 27 kDa   | 0.1 nM  | seeds   | [229]                   |
|                 | Trichosanthes anguina L.                     | Trichoanguin   | RIP 1      | 35 kDa   | 0.08 nM | seeds   | [231]                   |
|                 |                                              | SGSL           | lectin/ RIP 2 like | 62 kDa | n.a. 4 | seeds | [232–234]             |
|                 | Trichosanthes cordata Roxb.                  | TCA-I          | lectin     | 59 kDa   | n.a. 4 | seeds   | [235]                   |
|                 |                                              | TCA-II         | lectin     | 52 kDa   | n.a. 4 | seeds   | [235]                   |
Table 1. Cont.

| Family | Species ¹ | Protein             | Classific. | Mw ²   | IC₅₀ ³   | Source | References |
|--------|-----------|---------------------|------------|--------|---------|--------|------------|
|        | **Trichosanthes cucumerina L.** | **TCSL** | lectin/ RIP 2 candidate | 69 kDa | n.a. ⁴ | seeds | [236]    |
|        | **Trichosanthes cucumeroides (Ser.) Maxim.** | **β-trichosanthin = β-TCS** | RIP 1 | 28 kDa | 2.8 ng/mL; 0.1 nM | root tubers | [200,237,238] |
|        | | **α-kirilowin** | RIP 1 | 28.8 kDa | 1.2-1.8 ng/mL; 0.044–0.066 nM | seeds | [239] |
|        | | **β-kirilowin** | RIP 1 | 27.5 kDa | 1.8 ng/mL | seeds | [240] |
|        | | **β-trichosanthin = β-TCS** | RIP 1 | 26 kDa | 7 ng/mL | root tubers | [255] |
|        | | **γ-trichosanthin = γ-TCS** | RIP 1 | 26 kDa | 12 ng/mL | root tubers | [255] |
| Cucurbitaceae | **Trichosanthes kirilowii Maxim.** | **Trichosanthing = Trichosanthes antiviral protein = TAP = TCS = α-trichosanthin = α-TCS = GLQ223** | RIP 1 | 26–28 kDa | 6.1 ng/mL; 0.23 nM; 0.36 ng/mL; 1.31 nM | root tubers | [198,200,238,248–256] |
|        | | **Trichosanthing = Trichosanthes antiviral protein = TAP** | RIP 1 | 25 kDa | n.a. ⁴ | root tubers | [257] |
|        | | **β-trichosanthin = β-TCS** | RIP 1 | 26 kDa | 7 ng/mL | root tubers | [255] |
|        | | **γ-trichosanthin = γ-TCS** | RIP 1 | 26 kDa | 12 ng/mL | root tubers | [255] |
|        | | **Trichokirin S1** | sRIP 1 | 11,426 Da | 0.7 nM | seeds | [258] |
|        | | **S-Trichokirin** | sRIP 1 | 8 kDa | 115 pM | seeds | [259] |
|        | | **Trichosanthing** | sRIP 1 | 10,964 Da | 1.6 ng/mL | seeds | [256] |
|        | | **TKL-1 = Trichosanthes kirilowii lectin-1** | lectin/ RIP 2 candidate | 60 kDa | n.a. ⁴ | root tubers | [260,261] |
|        | | **TK-1** | lectin | n.a. ⁴ | - | root tubers | [262,263] |
|        | | **TK-II** | lectin | n.a. ⁴ | - | root tubers | [262,263] |
|        | | **TK-III** | lectin | n.a. ⁴ | - | root tubers | [262,263] |
|        | | **Trichosanthes kirilowii lectin** | lectin | 57 kDa | - | seeds | [264] |
Table 1. Cont.

| Family               | Species 1                           | Protein  | Classification | Mw 2 | IC₅₀ 3 | Source | References                  |
|----------------------|-------------------------------------|----------|----------------|------|--------|--------|----------------------------|
| Cucurbitaceae        | *Trichosanthes kirilowii* Maximovicz var. *japonica* (Miquel) Kitamura | Karasurin-A | RIP 1           | 27,215 Da | 0.1–0.3 ng/mL | root tubers | [265–268] |
|                      |                                     | Karasurin-B | RIP 1           | 27,214 Da | 0.1–0.3 ng/mL | root tubers | [267] |
|                      |                                     | Karasurin-C | RIP 1           | 27,401 Da | 0.1–0.3 ng/mL | root tubers | [267] |
|                      | *Trichosanthes lepiniate*           | Trichomaglin | RIP 1           | 24,673 Da | 10.1 nM | root tuber | [269] |
|                      | *Trichosanthes dioica* Roxb.        | TDSL      | lectin/         | 55 kDa | n.a. 4 | seeds    | [270] |
|                      |                                     |           | RIP 2 candidate |        |        |          |          |
|                      | *Trichosanthes* sp. Bac Kan 8-98    | Trichobakin | RIP 1           | 27 kDa | 3.5 pM | leaves   | [271] |
| Cupressaceae         | *Thuja occidentalis* L.             | Arbovitae RIP | RIP candidate | n.a. 4 | n.a. 4 | seeds    | [272] |
|                      | *Croton tiglium* L.                 | Crotin I  | RIP 1 candidate | 40 kDa | n.a. 4 | seeds    | [273–275] |
|                      |                                     | Crotin 2  | RIP 1           | n.a. 4 | n.a. 4 | seeds    | [276–278] |
|                      | *Euphorbia characias* L.            | E. characias lectin | lectin  | 80 kDa | -      | latex    | [279] |
|                      | *Suregada multiflora* (A.Juss.)     | Gelonin = GAP 31 | RIP 1 | 30–31 kDa | 0.406 ng/mL; 0.32 nM | seeds | [126,280–283] |
| Baill. [Syn.: *Gelonium multiflorum* A.Juss.] |                      |                      |        |        |          |          |
| Euphorbiaceae        | *Hura crepitans* L.                | Crepitin  | lectin         | n.a. 4 | n.a. 4 | latex    | [279] |
|                      | *Hura crepitans* RIP-5              | Crepitin  | lectin         | n.a. 4 | n.a. 4 | latex    | [285,286] |
|                      | *Hura crepitans* latex lectin       | Hurin     | lectin         | 70 kDa | -      | seeds    | [287,288] |
|                      | *Hura crepitans* seed lectin        | Hurin     | lectin         | 120 kDa | -      | seeds    | [286] |
|                      | *Jatropha curcas* L.                | Curcin    | RIP 1           | 28.2 kDa | 0.42 nM | seeds    | [273,289] |
|                      | *Jatropha curcas*                   | Curcin 2  | RIP 1           | 30.1 kDa | n.a. 4 | recomb. 6 | [290,291] |
|                      |                                    | Curcin-L  | RIP 1           | 32 kDa | 4 µg/mL | leaves   | [292,293] |
|                      | *Manihot palmata* Müll. Arg.        | Mapalmin  | RIP 1           | 32.3 kDa | 0.05 nM | seeds    | [113] |
| Family                | Species 1                        | Protein | Classific. | Mw 2 | IC₅₀ 3 | Source | References       |
|----------------------|----------------------------------|---------|------------|------|--------|--------|------------------|
| Euphorbiaceae        | Manihot esculenta Crantz. [Syn.: Manihot utilissima Pohl] | Manutin 1 | RIP 1      | n.a. 4 | 0.05 nM | seeds | [284,295]        |
|                      |                                  | Manutin 2 | RIP 1      | n.a. 4 | 0.12 nM | seeds | [295]            |
|                      |                                  | Ricin    | RIP 2      | 62.8 kDa | 0.14 nM | seeds | [59,281,296–309] |
|                      |                                  |          |            |       | 814 pM; 5.5 ng/mL |       |                  |
|                      |                                  | Ricin E  | RIP 2      | 64 kDa  | n.a. 4  | seeds | [310–312]        |
| Euphorbiaceae        | Ricinus communis L.              | RCA     | RIP 2      | 118–130 kDa | n.a. 4 | seeds | [303,313–321]    |
|                      |                                  |          |            |       |         |       |                  |
|                      |                                  | RCA     | RIP 2      | 60 kDa  | n.a. 4  | seeds | [313,314,316,317]|
|                      |                                  |          |            |       |         |       |                  |
| Fabaceae             | Abrus precatorius L.             | Abrin    | RIP 2      | 260 kDa | 0.5 nM | seeds | [29,307,315,323,325–330] |
|                      |                                  | Abrin-a  | RIP 2      | 63–65.5 kDa | 60 pM | seeds | [331–340]        |
|                      |                                  | Abrin-b  | RIP 2      | 67 kDa  | n.a. 4  | seeds | [333–335,338]    |
|                      |                                  | Abrin-c  | RIP 2      | 60.1–62.5 kDa | n.a. 4 | seeds | [331,332,334–337]|
|                      |                                  | Abrin-d  | RIP 2      | 67 kDa  | n.a. 4  | seeds | [334,335,338]    |
|                      |                                  | Abrin-II | RIP 2      | 63 kDa  | n.a. 4  | seeds | [337]            |

**Table 1. Cont.**
Table 1. Cont.

| Family          | Species 1 | Protein                      | Classific. | Mw 2   | IC₅₀ 3 | Source | References          |
|-----------------|-----------|------------------------------|------------|--------|-------|--------|---------------------|
| Fabaceae        | Abraș precatorius L. | APA = Abraș precatorius agglutinin = Abraș lectin = AAG | RIP 2      | 126–134 kDa | 3.5 nM | seeds  | [315,334, 341–345] |
|                 |           | APA-I                        | RIP 2      | 130 kDa  | n.a. 4| seeds  | [337,346]          |
|                 |           | APA-II                       | RIP 2      | 128 kDa  | n.a. 4| seeds  | [337]              |
|                 |           | Pulchellin                   | RIP 2      | 62 kDa   | n.a. 4| seeds  | [347–349]          |
|                 |           | Pulchellin PI                | RIP 2      | 61.5–63 kDa | n.a. 4| seeds  | [350]              |
|                 |           | Pulchellin PII               | RIP 2      | 61.5–63 kDa | n.a. 4| seeds  | [350]              |
|                 |           | Pulchellin PIII              | RIP 2      | 61.5–63 kDa | n.a. 4| seeds  | [350]              |
|                 | Iris hollandica var. Professor Blauw | IrisRIP = IRIP | RIP 1      | 28 kDa   | 0.1–0.16 nM | bulbs  | [353,354]         |
|                 |           | IrisRIP.A1                   | RIP 1      | 29 kDa   | 0.16 nM| bulbs  | [353]              |
|                 |           | IrisRIP.A2                   | RIP 1      | 29 kDa   | 0.12 nM| bulbs  | [353]              |
|                 |           | IrisRIP.A3                   | RIP 1      | 29 kDa   | 0.10 nM| bulbs  | [353]              |
|                 |           | IRA                          | RIP 2      | 60.4 kDa | n.a. 4| bulbs  | [355]              |
|                 |           | IRAb                         | RIP 2      | 65 kDa   | n.a. 4| bulbs  | [356,357]          |
|                 |           | IRAr                         | RIP 2      | 65 kDa   | n.a. 4| bulbs  | [356]              |
| Lamiaceae       | Clerodendrum aculeatum (L.) Schltdl. | CA-SRI | RIP 1 candidate | 34 kDa | <0.01 nM | leaves | [358,359]         |
|                 |           | CIP-29                       | RIP 1      | 29 kDa   | 0.548 nM; 16 ng/mL | leaves | [360,361]         |
|                 |           | CIP-34                       | RIP 1 candidate | 34 kDa | 87.4 nM; 3 µg/mL | leaves | [360,361]         |
|                 | Leonurus japonicus Houtt. | Leonurin | RIP candidate | n.a. 4 | n.a. 4 | seeds  | [362]              |
| Lauraceae       | Cinnamomum bodinieri H. Lév. | Bodinierin | RIP 2 | 65 kDa | 1.2 nM (A) 3 | kernel | [363]              |
Table 1. Cont.

| Family       | Species \(^1\)                              | Protein | Classific. | Mw \(^2\) | IC\(_{50}\) \(^3\) | Source | References         |
|--------------|---------------------------------------------|---------|------------|-----------|---------------------|--------|---------------------|
| Lauraceae    | *Cinnamomum camphora* (L.) J.Presl         | Camphorin | RIP 1      | 23 kDa    | 0.098 nM            | seeds  | [364,365]          |
|              |                                              | Cinnamomin | RIP 2      | 61 kDa    | 9.7 nM (A) \(^3\)  | seeds  | [364–367]          |
|              |                                              | Cinnamomin 1 | RIP 2      | 61 kDa    | n.a. \(^4\)         | seeds  | [364]              |
|              |                                              | Cinnamomin 2 | RIP 2      | n.a. \(^4\) | n.a. \(^4\)        | seeds  | [364]              |
|              |                                              | Cinnamomin 3 | RIP 2      | n.a. \(^4\) | n.a. \(^4\)        | seeds  | [364]              |
|              |                                              | Cinphorin  | sRIP 2     | 46 kDa    | 1.2 nM             | seeds  | [367,368]          |
|              | *Cinnamomum parthenoxylon* (Jack) Meisn.    | Porrectin | RIP 2      | 64.5 kDa  | 0.11 µM            | seeds  | [369]              |
|              | [Syn.: *Cinnamomum porrectum* (Roxb.) Kosterm.] |          |            |           |                    |        |                     |
| Malvaceae    | *Abelmoschus esculentus* (L.) Moench       | Abelesculin | RIP 1      | 30 kDa    | n.a. \(^4\)        | seeds  | [370]              |
|              | *Boerhaavia diffusa* L.                     | Boerhaavia inhibitor | RIP 1 candidate | 16–20 kDa | n.a. \(^4\) | roots | [371–373] |
|              |                                              | BAP I    | RIP 1      | 28 kDa    | n.a. \(^4\)        | roots  | [374]              |
|              | *Bougainvillea spectabilis* Willd.          | Bouganin | RIP 1      | 26.2 kDa  | 10.5 ng/mL          | leaves | [120,375]          |
|              |                                              | Bouganin | RIP 1      | 26.2 kDa  | 10.5 ng/mL          | leaves | [120,375]          |
|              |                                              | BBP-24   | RIP 1      | 24 kDa    | n.a. \(^4\)        | leaves | [376,377]          |
|              |                                              | BBP-28   | RIP 1      | 28 kDa    | n.a. \(^4\)        | leaves | [376,377]          |
| Nyctaginaceae| *Bougainvillea × buttiana* cv. Enid Lancaster | BBAP1    | RIP 1      | 35.49 kDa | n.a. \(^4\)        | leaves | [378,379]          |
|              | *Mirabilis expansa* (Ruiz & Pav.) Standl. | ME1      | RIP 1      | 29,208 Da | n.a. \(^4\)        | roots  | [380,381]          |
|              |                                              | ME2      | RIP 1      | 27 kDa    | n.a. \(^4\)        | roots  | [380]              |
|              | *Mirabilis jalapa* L.                       | MAP      | RIP 1      | 27,788 Da | 5.4 ng/mL           | roots/seeds | [373,382,383]      |
|              |                                              | MAP-2    | RIP 1      | 30,412 Da | 41.4 ng/mL          | seeds  | [383]              |
|              |                                              | MAP-3    | RIP 1      | 29,771 Da | 13.3 ng/mL          | seeds  | [383]              |
|              |                                              | MAP-4    | RIP 1      | 29,339 Da | 15.3 ng/mL          | seeds and leaves | [383] |
|              |                                              | MAP-S    | RIP 1      | 27,789 Da | n.a. \(^4\)        | seeds  | [146]              |
| Olacaceae    | *Malania oleifera* Chun & S. K. Lee         | Malanin  | lectin/ RIP 2 candidate | 61875 Da | n.a. \(^4\)        | seeds  | [384]              |

\(^1\) Family abbreviations: **Lauraceae**, **Malvaceae**, **Nyctaginaceae**, **Olacaceae**

\(^2\) Mw: Molecular weight

\(^3\) IC\(_{50}\): Inhibitory concentration 50%

\(^4\) n.a.: Not available
Table 1. Cont.

| Family          | Species                  | Protein            | Classification | Mw | IC₅₀ | Source       | References |
|-----------------|--------------------------|--------------------|----------------|----|------|--------------|------------|
| Olacaceae       | Ximenia americana L.     | Riproximin = Rpx   | RIP 2          | 56 kDa | n.a. | fruit kernels | [385,386]  |
|                 |                          | Rpx-I              | RIP 2          | 50 kDa | n.a. | fruit kernels | [386]      |
|                 |                          | Rpx-II             | RIP 2          | 53 kDa | n.a. | fruit kernels | [386]      |
| Passifloraceae  | Adenia digitata (Harv.) Engl. | Modeccin = Modeccin 4B | RIP 2          | 57–63 kDa | 4 µg/mL; 2.52 µg/mL; 2.52 µg/mL; 66 ng/mL (A) | roots | [387–390]  |
|                 |                          | Modeccin 6B        | RIP 2          | 57 kDa | 0.31 µg/mL | roots | [390]      |
|                 | Adenia ellenbeckii Harms | A. ellenbeckii lectin | RIP 2 candidate | 60 kDa | 10.1 µg/mL; 1.2 µg/mL (A) | caudex | [45]      |
|                 | A. fruticosa Burtt Davy  | A. fruticosa lectin | lectin         | 30 kDa | >100 µg/mL | caudex | [45]      |
|                 | A. glauca Schinz         | A. glauca lectin   | RIP 2 candidate | n.a. | >10 µg/mL; >5 µg/mL (A) | caudex | [45]      |
|                 | Adenia goetzei Harms (unresolved name) | A. goetzei lectin | RIP 2          | 60 kDa | 55.1 µg/mL; 0.7 µg/mL (A) | caudex | [45]      |
|                 | A. keramanthus Harms     | A. keramanthus lectin | RIP 2 candidate | 60–65 kDa | 10.0 µg/mL; 1.1 µg/mL (A) | caudex | [45]      |
|                 | Adenia lanceolata Engl.  | Lanceolin          | RIP 2          | 60 kDa | 5.2 µg/mL; 1.1 µg/mL (A) | caudex | [45,391,392] |
|                 | Adenia racemosa W. J. de Wilde | A. racemosa lectin | lectin         | 30 kDa | >400 µg/mL | caudex | [45]      |
|                 | A. spinosa Burtt Davy    | A. spinosa lectin  | RIP 2 candidate | n.a. | 4.7 µg/mL; 0.8 µg/mL (A) | caudex | [45]      |
|                 | A. stenodactyla Harms    | Stenodactylin      | RIP 2          | 60 kDa | 5.6 µg/mL; 0.5 µg/mL (A) | caudex | [45,391,392] |
|                 | A. venenata Forsk.       | A. venenata lectin | RIP 2 candidate | 60 kDa | 2.4 µg/mL; 0.4 µg/mL (A) | caudex | [45]      |
|                 | Adenia volkensii Harms   | Volkensin          | RIP 2          | 62 kDa | 5 µg/mL; 84 nM; 0.37 nM (A); 22 ng/mL (A); 7.5 µg/mL; 0.66 µg/mL (A) | roots | [45,393–395] |
Table 1. Cont.

| Family         | Species ¹   | Protein | Classif. | Mw ²      | IC₅₀ ³ | Source | References          |
|----------------|-------------|---------|----------|-----------|-------|--------|---------------------|
| α-PAP          | RIP 1       | 33,068 kDa | n.a. ⁴   | recomb. ⁶ | [396,397] |
| PAP            | RIP 1       | 29–30 kDa  | 0.29 nM  | leaves    | [29,398–403] |
| Phytolacca     | americana L.|         |          |           |       |        |                     |
| Phytolacceae   | Phytolacca  |         |          |           |       |        |                     |
| PAP-I          | RIP 1       | 30 kDa   | 2 pM     | spring leaves | [404] |
| PAP-II         | RIP 1       | 30–31 kDa | 4 pM     | early summer leaves | [399,400, 404,405] |
| PAP-III        | RIP 1       | 30 kDa   | 3 pM     | late summer leaves | [404] |
| PAP-C          | RIP 1       | 29 kDa   | 0.062 nM; 2 ng/mL | cell cultures | [406] |
| PAP-H          | RIP 1       | 29.5 kDa | n.a. ⁴   | hairy roots | [407] |
| PAP-R          | RIP 1       | 29.8 kDa | 0.05 nM  | roots     | [113] |
| PAP-S          | RIP 1       | 30 kDa   | 36–83 nM; 1.09–2.5 ng/mL | seeds | [399,408] |
| PAP-S1         | RIP 1       | n.a. ⁴   | n.a. ⁴   | recomb. ⁶ | [397] |
| PAP-S2         | RIP 1       | n.a. ⁴   | n.a. ⁴   | recomb. ⁶ | [397] |
| Diocin 1       | RIP 1       | 30,047 Da | 19.74 ng/mL; 0.658 nM | leaves of young plants | [409] |
| Diocin 2       | RIP 1       | 29,910 Da | 6.85 ng/mL; 0.229 nM | leaves of young plants | [409] |
| PD-L1          | RIP 1       | 32,715 Da | 102 pM; 3.32 ng/mL; 8.5 pM | leaves | [410,411] |
| PD-L2          | RIP 1       | 31,542 Da | 110 pM; 3.46 ng/mL | leaves | [410,412] |
| PD-L3          | RIP 1       | 30,356 Da | 228 pM; 6.93 ng/mL | leaves | [410,412] |
| PD-L4          | RIP 1       | 29185 Da | 134 pM; 3.92 ng/mL | leaves | [410,413] |
| PD-S1          | RIP 1       | 30.9 kDa | 0.12 nM  | seeds | [414] |
| PD-S2          | RIP 1       | 29,586 Da | 0.06 nM  | seeds | [414,415] |
| PD-S3          | RIP 1       | 32 kDa   | 0.08 nM  | seeds | [414] |
| Family            | Species 1                  | Protein                  | Classified | Mw 2 | IC<sub>50</sub> 3 | Source | References |
|-------------------|---------------------------|--------------------------|------------|------|------------------|--------|------------|
| Phytolaccaceae    | *Phytolacca dodecandra* L’Hér. | Dodecandrin              | RIP 1      | 29 kDa | n.a. 4          | leaves | [416,417] |
|                   |                           | Dodecandrin C            | RIP 1      | 31–32 kDa | n.a. 4     | cell cultures | [417]     |
|                   | *Phytolacca heterotepala* H. Walter | Heterotepalin 4         | RIP 1      | 29,326 Da | 82 pM      | leaves  | [418]     |
|                   |                           | Heterotepalin 5b         | RIP 1      | 30,477 Da | 52 pM      | leaves  | [418]     |
| Phytolacca insularis Nakai |                    | Insularin               | RIP 1      | 31 kDa  | n.a. 4     | recomb. 6 | [7,419]  |
|                   |                           | = P. insularis antiviral protein |          |         |             |         |           |
|                   |                           | = PIP                   | RIP 1      | 30 kDa  | 0.47 nM   | seeds   | [281,421–424] |
| Poaceae           | *Hordeum vulgare* L.     | Barley toxin             | RIP 1      | 30 kDa  | 25 ng/mL   | seeds   | [422]     |
|                   |                           | = Barley translation inhibitor |          |         |             |         |           |
|                   |                           | = Barley Protein Synthesis Inhibitor |          |         |             |         |           |
|                   |                           | = BPSI                  | RIP 1      | 30 kDa  | 25 ng/mL   | seeds   | [281,421, 422,425] |
|                   |                           | = RIP 30                | RIP 1      | 29,836 Da | 25 ng/mL  | seeds   | [281,422] |
|                   |                           | Barley toxin I          | RIP 1      | 30 kDa  | 25 ng/mL   | seeds   | [421]     |
|                   |                           | = Barley translation inhibitor I |          |         |             |         |           |
|                   |                           | = Barley Protein Synthesis Inhibitor II |          |         |             |         |           |
|                   |                           | = BPSI II               | RIP 1      | 30 kDa  | 15 ng/mL   | seeds   | [281,422] |
|                   |                           | Barley toxin III        | RIP 1      | 30 kDa  | 15 ng/mL   | seeds   | [281,422] |
|                   |                           | = Barley translation inhibitor III |          |         |             |         |           |
|                   |                           | JIP60                   | RIP 3/peculiar | 60 kDa  | n.a. 4     | recomb. 6 | [5,426]  |
| Family             | Species 1 | Protein         | Classific. | Mw 2  | IC<sub>50</sub> 3 | Source | References |
|-------------------|-----------|-----------------|------------|-------|-----------------|--------|------------|
| Poaceae           | Oryza sativa L. | Oryza sativa RIP | RIP 1      | 27 kDa | n.a. 4          | recomb. 6 | [427]       |
| Secale cereale L. | Oryza sativa | RIP 1           | 30,171 Da  | 0.42 µg/mL | seeds          |        | [421,428]  |
|                   | Tritin    | RIP 1           | 30 kDa     | n.a. 4 | germ            | [421,429–431] |
|                   | Tritin 1  | RIP 1           | 30 kDa     | 250 ng/mL | whole wheat    | [432]  |
|                   | Tritin 2  | RIP 1           | 30 kDa     | 250 ng/mL | whole wheat    | [432]  |
|                   | Tritin 3  | RIP 1           | 30 kDa     | 250 ng/mL | whole wheat    | [432]  |
|                   | Tritin-S  | RIP 1           | 32.1–32.8 kDa | n.a. 4 | seeds           | [433]  |
|                   | Tritin-L  | RIP 1           | 37.0–37.9 kDa | n.a. 4 | leaves          | [433]  |
|                   | b-32      | RIP 3/peculiar  | 34 kDa     | 28–60 pM; 0.7–1.5 ng/mL; 0.065 nM | seeds | [4,434–438] |
|                   | = maize RIP | RIP 1          |            |       |                 |        |            |
|                   | = maize proRIP1 | RIP 1     |            |       |                 |        |            |
|                   | Maize proRIP2 | RIP 3/peculiar | 31.1 kDa       | n.a. 4 | recomb. 6      | [436,437] |
|                   |           | RIP 1           |            |       |                 |        |            |
| Ranunculaceae     | Eranthis hyemalis (L.) Salis. | EHL | RIP 2 | 62 kDa | n.a. 4 | root tubers | [439,440] |
| Santalaceae       | Phoradendron californicum Nutt. | PCL | RIP 2 | 69 kDa | n.a. 4 | n.n | [441] |
|                   | Viscum album L. (Himalayan mistletoe) | HmRip | RIP 2 | 65 kDa | n.a. 4 | leaves | [442–444] |
|                   |           | HmRip 1         | RIP 2 | 65 kDa | n.a. 4 | leaves | [442–444] |
|                   |           | HmRip 2         | RIP 2 | 65 kDa | n.a. 4 | leaves | [442–444] |
|                   |           | HmRip 3         | RIP 2 | 65 kDa | n.a. 4 | leaves | [442–444] |
|                   |           | HmRip 4         | RIP 2 | 65 kDa | n.a. 4 | leaves | [442–444] |
| Santalaceae       | Viscum album L. (European mistletoe) | ML-I = Mistletoe lectin I | RIP 2 | 115–125 kDa | 2.6 µg/mL; 0.21 µg/mL (A) 5; 3.7 pM (A) 5 | leaves | [234,445–454] |
|                   |           | ML-II = Mistletoe lectin II | RIP 2 | 60–64 kDa | n.a. 4 | leaves | [448,450–452] |
|                   |           | ML-III = Mistletoe lectin III | RIP 2 | 50–61 kDa | n.a. 4 | leaves | [448,450–452] |
Table 1. Cont.

| Family         | Species 1 | Protein | Classif. | Mw 2 | IC₅₀ 3 | Source   | References |
|----------------|-----------|---------|----------|------|--------|----------|------------|
| Santalaceae    | *Viscum articulatum* Burm. f. | Articulatin-D | RIP 2 | 66 kDa | n.a. 4 | whole plant | [455] |
|                | *Viscum coloratum* (Kom.) Nakai | KML | RIP 2 | n.a. 4 | n.a. 4 | leaves | [456] |
|                | [Syn.: *Viscum album* subsp. coloratum Kom.] | KML-C | RIP 2 | 59.5 kDa | n.a. 4 | leaves | [454,457] |
|                |           | KML-IIL | RIP 2 | 60 kDa | n.a. 4 | leaves | [457] |
|                |           | KML-IIU | RIP 2 | 64 kDa | n.a. 4 | leaves | [457] |
|                |           | VCA | RIP 2 | 60 kDa | n.a. 4 | leaves | [458,459] |
| Solanaceae     | *Nicotiana tabacum* L. | CIP31 | RIP-like protein | 31 kDa | n.a. 4 | leaves | [460] |
|                |           | TRIP | RIP 1 candidate | 26 kDa | 100 ng/mL | leaves | [461] |
| Thymelaeaceae  | *Phaleria macrocarpa* (Scheff.) Boerl. | P. macrocarpa | RIP candidate | n.a. 4 | n.a. 4 | seeds | [462] |

1 For the botanical name of the plant species we chose the current accepted name from www.theplantlist.org. In some cases, there is also given a synonym, because the protein/RIP is derived from that synonym that is given in the corresponding reference; 2 For the values of molecular weight (Mw) we listed the latest values from the native unreduced proteins obtained from gel filtration or from SDS-PAGE. If there were too many different values from different authors, we listed a range. We listed the exact value obtained from MALDI-TOF, ESI-TOF or Q-TOF, if this was available; 3 IC₅₀ is the half minimal inhibitory concentration (50%) of the protein, which inhibits translation from a cell free system using rabbit reticulocyte lysate. For the IC₅₀ values, we listed the values of the molar mass or concentration in mg/mL. In some cases, there were many different values from different laboratories that led us to list a range; 4 n.a. = not available; in the case of IC₅₀ values there are several reasons for n.a.: 1. The translation-inhibitory assay was not performed; 2. The translation-inhibitory assay was performed by using another system than the cell free system with rabbit reticulocyte lysate, e.g., cancer cells; 3. The IC₅₀ values were specified with another unit, e.g., mg/kg; 5 (A) = A-chain; the IC₅₀ value followed by (A) is for the reduced type 2 RIP; 6 recom. = recombinant; Proteins obtained through biotechnological procedures.

3. Exceptions Prove the Rule

To be classified as “classical” type 1 or type 2 RIP, a protein needs both the structure and the N-glycosidase activity including the conserved amino acid residues, which are believed to be present in all RIPS, of the putative active site region [94,101,463]. This active site region is also known as shiga/ricin toxic domain [106]. Beside the peculiar type 1 RIPS, b-32 and JIP60, there is a certain amount of other proteins that cannot be grouped into the classical type 1 or type 2 RIPS, because of structural and functional differences.

3.1. Small RIPS

First of all, there are “small type 1 RIPS” (sRIP 1; Table 2), which are single chain proteins exhibiting N-glycosidase activity with a smaller molecular weight than the classical type 1 RIPS. Interestingly, all known small type 1 RIPS are synthesized by plants belonging to the family Cucurbitaceae. α-luffin and β-luffin from Luffa cylindrica indeed have the same size as the other small type 1 RIPS, but because of
their lower toxicity of 17 µM and 300 nM, respectively, and due to the unknown mechanism of action, they are classified as “small type 1 RIP candidates” (Table 3). Also luffin-S, luffinS(1), luffinS(2), and luffinS(3) have similar sizes as the other small type 1 RIPS and all of them inhibit protein synthesis in a cell-free system, but it was not analyzed, whether the translation-inhibitory is due to the N-glycosidase activity or not. In addition, a different mechanism of action was found for luffin-S [186]. For this reason, the luffinSs are considered as small type 1 RIP candidates (Table 3). Another small type 1 RIP candidate is cucurmoschin that was designated as an antifungal protein by the authors [160]. Cucurmoschin indeed inhibits protein synthesis in a cell-free system, but there was no homology with other type 1 RIPS or small type 1 RIPS concerning the amino acid sequence specified, but the fact that the N-glycosidase activity was neither verified nor excluded led us to the decision to classify cucurmoschin as a small type 1 RIP candidate. Lagenin, α-pisavin and β-pisavin have molecular weights of 20 kDa, 20.5 kDa and 18.7 kDa, respectively; thus, they differ from the classical type 1 RIPS as well as from the small type 1 RIPS. Lagenin inhibits cell-free translation in a rabbit reticulocyte system, but it was not clarified whether this is due to the N-glycosidase activity [171]. Because the size of lagenin is closer to the classical type 1 RIPS than to the biggest known small type 1 RIPS (α-benincasin and β-benincasin, both of them 12 kDa), lagenin should be classified as a type 1 RIP candidate. α-pisavin and β-pisavin have molecular weights that are also closer to the classical type 1 RIPS than to the small type 1 RIPS, but compared with lagenin, they both have the N-glycosidase activity and, in addition, show amino acid similarity with other type 1 RIPS. For that reason, α-pisavin and β-pisavin are considered type 1 RIPS.

Cinphorin is a type 2 RIP from the seeds of Cinnamomum camphora with a molecular weight of 46 kDa, which is due to the smaller A-chain than the other classical type 2 RIPS [368]. It is proposed that cinphorin is a cleaving product of cinnamomin, another type 2 RIP from Cinnamomum camphora, or its mRNA [367]. Cleaving processes during the evolution of RIPS are not unusual [29], but cinphorin is the only type 2 RIP with a smaller A-chain known to date, and, therefore, it is questionable whether it is necessary to denominate an extra classification for cinphorin. Considering that there might be more RIPS that are not detected to date, of which one could be another type 2 RIP with a smaller A-chain, however, we propose to classify cinphorin as a “small type 2 RIP” (sRIP 2).

### Table 2. Small RIPS.

| Protein       | Source                          | Mw    | Classification | References |
|---------------|---------------------------------|-------|----------------|------------|
| α-benincasin  | Benincasa hispida (Cucurbitaceae) | 12 kDa | sRIP 1         | [151]      |
| β-benincasin  | Benincasa hispida (Cucurbitaceae) | 12 kDa | sRIP 1         | [151]      |
| Charantin     | Momordica charantia (Cucurbitaceae) | 9.7 kDa | sRIP 1         | [216]      |
| Cinphorin     | Cinnamomum camphora (Lauraceae)  | 46 kDa | sRIP 2         | [367,368]  |
| Luffacyclin   | Luffa cylindrica (Cucurbitaceae)  | 7.8 kDa | sRIP 1         | [184]      |
| Luffangulin   | Luffa acutangula (Cucurbitaceae) | 5.6 kDa | sRIP 1         | [174]      |
| Luffin P1     | Luffa cylindrica (Cucurbitaceae)  | 5226.1 Da | sRIP 1     | [185]      |
| γ-momorcharin | Momordica charantia (Cucurbitaceae) | 11.5 kDa | sRIP 1     | [205]      |
| S-trichokirin | Trichosanthes kirilowii (Cucurbitaceae) | 8 kDa | sRIP 1     | [259]      |
| Trichokirin S1| Trichosanthes kirilowii (Cucurbitaceae) | 11426 Da | sRIP 1   | [258]      |
| Trichosanthrip| Trichosanthes kirilowii (Cucurbitaceae) | 10964 Da | sRIP 1   | [256]      |
Table 3. RIP candidates and RIP-like proteins.

| Protein          | Source                                | Mw    | IC₅₀             | Classification       | References |
|------------------|---------------------------------------|-------|------------------|----------------------|------------|
| *A. ellenbeckii* lectin | *Adenia ellenbeckii* (Passifloraceae) | 60 kDa | 10.1 µg/mL; 1.2 µg/mL | RIP 2 candidate      | [45]       |
| *A. glauca* lectin        | *Adenia glauca* (Passifloraceae)      | n.a.  | >10 µg/mL; >5 µg/mL | RIP 2 candidate      | [45]       |
| *A. keramanthus* lectin  | *Adenia keramanthus* (Passifloraceae) | 60–65 kDa | 10.0 µg/mL; 1.1 µg/mL | RIP 2 candidate      | [45]       |
| *A. spinosa* lectin       | *Adenia spinosa* (Passifloraceae)     | n.a.  | 4.7 µg/mL; 0.8 µg/mL | RIP 2 candidate      | [45]       |
| *A. venenata* lectin      | *Adenia venenata* (Passifloraceae)    | 60 kDa | 2.4 µg/mL; 0.4 µg/mL | RIP 2 candidate      | [45]       |
| Arborvitae RIP | *Thuja occidentalis* (Cupressaceae)    | n.a.  | n.a.             | RIP candidate        | [272]      |
| BDA              | *Bryonia crotica* subsp. *dioica*     | 61 kDa | >1500 nm         | RIP 2-like lectin    | [73,156]   |
| Boerhaavia inhibitor | *Boerhaavia diffusa* (Nyctaginaceae)  | 16–20 kDa | n.a.             | RIP 1 candidate      | [371–373] |
| CA-SRI           | *Clerodendrum aculeatum* (Lamiaceae)  | 34 kDa | <0.01 nM         | RIP 1 candidate      | [358,359] |
| CF-RIP           | *Cucumis ficifolius* (Cucurbitaceae)  | n.a.  | n.a.             | RIP 1 candidate      | [159]      |
| CIP-34           | *Clerodendrum inerme* (Lamiaceae)     | 34 kDa | 87.4 nM; 3 µg/mL  | RIP 1 candidate      | [360,361] |
| CIP31            | *Nicotiana tabacum* (Solanaceae)      | 31 kDa | n.a.             | RIP 1-like protein   | [460]      |
| Crotin I         | *Croton tiglium* (Euphorbiaceae)      | 40 kDa | n.a.             | RIP 1 candidate      | [273,275] |
| Cucurmoschin     | *Cucurbita maxima* (Cucurbitaceae)    | 9 kDa  | 1.2 µM           | small RIP 1 candidate| [160]      |
| Foetidissimin    | *Cucurbita foetidissima* (Cucurbitaceae) | 63 kDa | 25.9 nM         | peculiar RIP 2       | [157]      |
| Lagenin          | *Lagenaria siceraria* (Cucurbitaceae) | 20 kDa | 0.21 nM          | RIP 1 candidate      | [171]      |
| Leonurin         | *Leonurus japonicus* (Laminariaceae)  | n.a.  | n.a.             | RIP candidate        | [362]      |
| Luffin-S         | *Luffa cylindrica* (Cucurbitaceae)    | 10 kDa | 0.34 nM          | small RIP 1 candidate| [186]      |
| LuffinS(1)       | *Luffa cylindrica* (Cucurbitaceae)    | 8 kDa  | 130 nM           | small RIP 1 candidate| [187]      |
| LuffinS(2) = luffin S2 | *Luffa cylindrica* (Cucurbitaceae)   | 7.8 kDa | 10 nM            | small RIP 1 candidate| [187,188] |
| LuffinS(3)       | *Luffa cylindrica* (Cucurbitaceae)    | 8 kDa  | 630 nM           | small RIP 1 candidate| [187]      |
| Malanin          | *Malania oleifera* (Olacaceae)        | 61,875 Da | n.a.          | lectin/RIP 2 candidate| [384]      |
| ε-momorcharin    | *Momordica charantia* (Cucurbitaceae) | 24 kDa | 170 nM          | RIP 1 candidate      | [203]      |
| α-moschin        | *Cucurbita moschata* (Cucurbitaceae)  | 12 kDa | 17 µM           | small RIP 1 candidate| [168]      |
| β-moschin        | *Cucurbita moschata* (Cucurbitaceae)  | 12 kDa | 300 nM          | small RIP 1 candidate| [168]      |
| Panaxagin        | *Panax ginseng* (Araliaceae)          | 52 kDa | 0.28 nM         | peculiar RIP 1 candidate/RNase| [110]      |
| *P. macrocarpa* RIP | *Phaleria macrocarpa* (Thymelaceae)   | n.a.  | n.a.             | RIP candidate        | [462]      |
| Quinqueginsins   | *Panax quinquefolius* (Araliaceae)    | 53 kDa | 0.26 nM         | peculiar RIP 1 candidate/RNase| [111]      |
| Sativin          | *Pisum sativum* var. *macrocarpon* (Fabaceae) | 38 kDa | 14 µM          | RIP 1 candidate      | [352]      |
| SGSL             | *Trichosanthes anguina* (Cucurbitaceae) | 62 kDa | n.a.             | RIP 2-like lectin    | [234]      |
Table 3. Cont.

| Protein | Source                        | Mw     | IC<sub>50</sub> | Classification     | References |
|---------|-------------------------------|--------|-----------------|-------------------|------------|
| SoRIP2  | Spinacia oleracea (Amaranthaceae) | 36 kDa | n.a.            | RIP 1 candidate   | [106,107]  |
| TCSL    | Trichosanthes cucumerina (Cucurbitaceae) | 69 kDa | n.a.            | lectin/RIP 2 candidate | [236]    |
| TDSL    | Trichosanthes dioica (Cucurbitaceae) | 55 kDa | n.a.            | lectin/RIP 2 candidate | [270]    |
| TKL-1   | Trichosanthes kirilowii (Cucurbitaceae) | 60 kDa | n.a.            | lectin/RIP 2 candidate | [260]    |
| TRIP    | Nicotiana tabacum (Solanaceae)  | 26 kDa | 100 ng/mL       | RIP 1 candidate   | [461]    |

3.2. RIP Candidates and RIP-Like Proteins

There are four single chain proteins with a bigger molecular weight than the other type 1 RIPS: Jc-SCRIP from *Jatropha curcas* (38 kDa), β-nigritin from *Sambucus nigra* (40 kDa), sativin from *Pisum sativum* (38 kDa), and CIP-34 from *Clerodendrum inerme* (34 kDa). β-nigritin exhibits N-glycosidase activity and, therefore, it is classified as a classic type 1 RIP, because there are no further structural peculiarities [54]. Jc-SCRIP differs not only on the basis of the molecular weight from the other type 1 RIPS, but also with regard to its N-terminal amino acid sequence, acidic isoelectric point, high temperature stability, and high sugar content giving this protein additional lectin properties [294]. Because of those unique molecular characteristics, it might be classified as peculiar type 1 RIP as well as b-32 and JIP60. But that would make this issue unnecessarily complicated, because Jc-SCRIP does not have such structural differences compared to other type 1 RIPS like as b-32 and JIP60. Therefore, and because of its N-glycosidase activity, Jc-SCRIP is classified as a classical type 1 RIP. Compared with that, sativin and CIP-34 cannot be classified as classical type 1 RIPS, because, among other things, the N-glycosidase activity was not found, and, therefore, together with other proteins, they are referred to as “RIP candidates” or “RIP-like proteins” (Table 3). Sativin is considered to be a type 1 RIP candidate, because of its amino acid sequence similarity of 48% to α-pisavin and β-pisavin [352], which are classified as type 1 RIPS as mentioned above. CIP-34 is the major protein of a 100 kDa protein complex with an unknown structure [360]. In Girbès et al. [7], it is indeed classified as a classical type 1 RIP, but it might be better to assign CIP-34 to the peculiar type 1 RIPS, because it is larger than other type 1 RIPS and it consists of protein domains with an unknown structure and function. To be grouped into the RIPS, however, the N-glycosidase activity of CIP-34 has to be detected. Thus, it is classified as type 1 RIP candidate until further notice.

Panaxagin from *Panax ginseng* and quinqueginsin from *Panax quinquefolius* are two other proteins that differ from the classical type 1 RIPS with regard to molecular weight, structure, and functionality. Both panaxagin and quinqueginsin are homodimeric proteins with molecular weights of 52 kDa and 53 kDa, respectively [110,111]. The amino acid sequence of panaxagin and quinqueginsin show similarities with both RNases and type 1 RIPS, and on the basis of their high translation-inhibitory activities of 0.26 nM and 0.28 nM, respectively, they are classified as RIPS, where the authors proposed the denomination “dimeric type 1 RIP”. Due to their unusual dimeric structure, they can also be considered as peculiar type 1 RIPS. As mentioned above, the N-glycosidase activity of a protein needs to be detected in order to be classified as an RIP, but this was not possible for either panaxagin or quinqueginsin, because they both show strong RNase activity destroying the ribosomes. Therefore, both
panaxagin and quinqueginsin are considered as peculiar type 1 RIP candidates until the whole amino acid sequence is analyzed, which will or will not show the conserved amino acids of the active site region.

SoRIP2 from Spinacia oleraceae is a type 1 RIP candidate, because the N-glycosidase activity assay was not performed, but the amino acid sequence shows similarities to the shiga/ricin toxic domain [106]. Interestingly, SoRIP2 only shows low sequence similarity with SoRIP1, another protein from Spinacia oleraceae that is classified as type 1 RIP.

Boerhaavia inhibitor from Boerhaavia diffusa was described as a virus inhibitor without mentioning any more details about the inhibitory activity of rabbit reticulocyte lysate or N-glycosidase activity [371,372]. But the size of 16–20 kDa and the fact that antiserum against the type 1 RIP MAP from Mirabilis jalapa giving positive reaction with Boerhaavia diffusa extract [373], led us to the conclusion to denote Boerhaavia inhibitor as a RIP 1 candidate.

CA-SRI from Clerodendrum aculeatum is like Boerhaavia inhibitor an antiviral protein that induces systemic resistance [358]. Neither the inhibition of translation of rabbit reticulocyte lysate nor the N-glycosidase was demonstrated, but the size of 34 kDa and the amino acid sequence homology of 54% [359] to the type 1 RIP PAP from Phytolacca americana make CA-SRI a RIP 1 candidate.

CF-RIP is a type 1 RIP candidate from Cucumis ficifolius that was obtained by cloning and sequencing the cDNA [159]. To be classified as type 1 RIP, native CF-RIP has to be isolated as well as the N-glycosidase activity has to be detected. Compared with that, the enzymatic activity of ε-momorcharin from Momordica charantia indeed was detected, but it was not denominated as a classical type 1 RIP, because its IC50 of 170 nM is too low. Thus, the authors supposed significant structural dissimilarities of ε-momorcharin from the classical type 1 RIPs [203]. Another protein showing N-glycosidase activity, but is not classified as type 1 RIP, is TRIP from Nicotiana tabacum, because TRIP releases less adenine compared to type 1 RIPs [461]. It shows almost all the characteristics of type 1 RIPs instead of sequence similarity with other type 1 RIPs, wherein it should be mentioned that only 15 internal amino acids were analyzed. The authors classified TRIP as a RIP-like protein, but the fact that it shows superoxide dismutase activity, that is well known for RIPs [23], led us to the proposal to classify TRIP as a type 1 RIP candidate until the whole amino acid sequence is analyzed, which will or will not show the conserved amino acids of type 1 RIPs.

Because of cleaving supercoiled DNA by a crude extract of seeds from Phaleria macrocarpa, it was assumed that at least one RIP is included in this extract [462], but there were no more details given about this assumed RIP. The same applies to arborvitaes RIP, where it is only known that there is probably a RIP synthesized by arborvitaes [272], but we could only find the abstract of this paper during our investigation and in the abstract it is not clarified whether it is a RIP or just an RNase. Due to a lack of any further details, we propose to denominate these assumed RIPS as RIP candidates without mentioning the more detailed denomination RIP 1 or RIP 2 candidate. The same applies to leonurin from Leonurus japonicus, for which we did not find any further information as well [362].

As mentioned in the introduction, some lectins were found from several Adenia species [45], of which the lectins from Adenia lanceolata and from Adenia stenodactyla were classified later as
The heterodimeric type 2 RIPs represent the classical type 2 RIPs consisting of one A-chain and one B-chain linked together through a disulphide bridge [A-s-s-B]. Tetrameric type 2 RIPs consist of four protein chains and, therefore, the proposal was made to denominate these proteins as type 4 RIPs [306]. But that would mean that there are type 1, type 2, and type 4 RIPs, but no type 3 RIPs, because they were renamed peculiar type 1 RIPs, which may lead to confusion. Thus, we agree with the term “tetrameric type 2 RIPs”. These RIPs are subdivided
into two groups. One of those consist of two [A-s-s-B]-units linked together non-covalently, which can also be considered dimeric classical type 2 RIPs ([A-s-s-B]:). It should be mentioned that the [A-s-s-B]-units can be different, e.g., in RCA from *Ricinus communis* ([A-s-s-B],[A-s-s-B]; [316,323]). The other group of tetrameric type 2 RIPs includes proteins with an extra disulphide bond between the two B-chains [A-s-s-B-s-s-B-s-s-A]. In Ferreras *et al.* [72], SNA-I and SNA-If were grouped herein, but it was shown that both native SNA-I and native SNA-If occur as a 240 kDa protein having the structure [A-s-s-B-s-s-B-s-s-A]: [69]. Thus, these proteins can also be considered as dimeric tetrameric type 2 RIPs linked non-covalently, but we propose the denomination octameric type 2 RIPs. PMRIPt from *Polygonatum multiflorum* and abrin from *Abrus precatorius* are also octameric type 2 RIPs consisting of four [A-s-s-B]-units, which are linked non-covalently as well ([A-s-s-B]; [117,328]). They can also be considered as tetrameric classical type 2 RIPs.

Dimerization or oligomerization is a common behavior of purified and concentrated proteins. To avoid any confusion, the denomination of tetrameric type 2 RIPs with the structure [A-s-s-B]: and octameric type 2 RIPs is not meant as a real classification, because this would separate closely related type 2 proteins such as SNAI and SSA or abrin and pulchellin. We grouped those proteins in Table 4 as an addition to Table 1 to explain the bigger molecular weights and to show their native form in which they have been detected.

**Table 4.** Dimeric, tetrameric, and octameric type 2 RIPs and dimeric lectins.

| Structure          | Protein | Source                                | Mw       | References |
|--------------------|---------|---------------------------------------|----------|------------|
| Octameric          |         |                                       |          |            |
| [A-s-s-B-s-s-B-s-s-A]₂ | SNA-I   | Sambucus nigra (Adoxaceae)            | 240 kDa  | [66,69]    |
|                    | SNA-If  | Sambucus nigra (Adoxaceae)            | 240 kDa  | [69]       |
| Octameric          |         |                                       |          |            |
| [A-s-s-B]₄         | Abrin   | Abrus precatorius (Fabaceae)          | 260 kDa  | [328]      |
|                    | PMRIPt  | Polygonatum multiflorum (Asparagaceae)| 240 kDa  | [117]      |
| Tetrameric         |         |                                       |          |            |
| [A-s-s-B-s-s-B-s-s-A] | SNAfu-I | Sambucus nigra (Adoxaceae)            | subunits of 30–33 kDa | [71,72] |
|                    | SRA     | Sambucus sieboldiana (Adoxaceae)      | 120 kDa  | [79]       |
|                    | SSA     | Sambucus sieboldiana (Adoxaceae)      | 160 kDa  | [81]       |
|                    | APA     | Abrus precatorius (Fabaceae)          | 126–134 kDa | [315,341,342,345] |
|                    | *Hura crepitans* latex lectin | *Hura crepitans* (Euphorbiaceae) | 112 kDa  | [279]      |
| Tetrameric         |         |                                       |          |            |
| [A-s-s-B]₂         | MCL     | Momordica charantia (Cucurbitaceae)    | 115–124 kDa | [207,218–220] |
|                    | ML-I    | Viscum album (Santalaceae)             | 115–125 kDa | [445,447,450–452] |
|                    | Nigrin b| Sambucus nigra (Adoxaceae)             | 120 kDa  | [58]       |
|                    | Nigrin f | Sambucus nigra (Adoxaceae)             | 120 kDa  | [62]       |
|                    | SNA-I’  | Sambucus nigra (Adoxaceae)             | 120 kDa  | [67]       |
Table 4. Cont.

| Structure | Protein          | Source                      | Mw      | References |
|-----------|------------------|-----------------------------|---------|------------|
| Tetrameric | RCA              | Ricinus communis (Euphorbiaceae) | 118–130 kDa | [316,323] |
| [A-ss-B]₆[А-сс-В]₆ | E. characias lectin | Euphorbia characias (Euphorbiaceae) | 80 kDa | [279] |
|          | Luffa acutangula fruit lectin | Luffa acutangula (Cucurbitaceae) | 48 kDa | [175] |
| Homodimeric lectins | Protein fraction 1 | Momordica charantia (Cucurbitaceae) | 49 kDa | [224] |
| [B]₂ | Protein fraction 2 | Momordica charantia (Cucurbitaceae) | 49 kDa | [224] |
|          | Sechium edule fruit lectin | Sechium edule (Cucurbitaceae) | 44 kDa | [230] |
|          | SELld | Sambucus ebulus (Adoxaceae) | 67,906 Da | [52] |
|          | SELfd | Sambucus ebulus (Adoxaceae) | 68 kDa | [47] |
|          | SNAld | Sambucus nigra (Adoxaceae) | n.a. | [63] |

3.4. Non-Toxic Type 2 RIPS

For a long time, all type 2 RIPS were considered to be highly potent toxins, but, to date, there are also known type 2 RIPS, which are not or only less toxic \textit{in vivo}, and therefore they are denominated as non-toxic type 2 RIPS (reviewed in [7,8], not listed in this review). Nearly all of them have lectin properties and show \textit{N}-glycosidase activity in a cell-free system, so that these characteristics cannot be the reason for the missing \textit{in vivo}-toxicity. SNLRP1 from \textit{Sambucus nigra} for instance is a non-toxic type 2 RIP without lectin properties. On the other hand, nigrin b from \textit{Sambucus nigra} has lectin properties but is non-toxic as well, because it is degraded rapidly and excreted by cells [8]. Articulatin D from \textit{Viscum articulatum} is another type 2 RIP without lectin properties, but compared to SNLRP1, articulatin D is very toxic [455]. Thus, these examples show that the reasons for the vast differences in toxicity are not clearly understood. Nevertheless, non-toxic type 2 RIPS are quite interesting for anti-cancer therapy, because they may have a lower potential of side effects.

3.5. Demotion of Some RIPS

At last, it should be mentioned that there are some proteins, which were first classified as RIPS, but it was later shown that they act with a different mechanism of action for inhibiting translation than \textit{N}-glycosidase. Melonin from \textit{Cucumis melo} was first classified as type 1 RIP [465], but a few years later, it was found that it is a ribonuclease (RNase) that specifically degrades poly(C)- and cytidine-containing bonds [466]. Crotin I and crotin II, two proteins from \textit{Croton tiglium}, were classified as type 1 RIPS as well [7], but for crotin II, it was found that it belongs to RNA hydrolases, which cleave a phosphodiester bond between G₄₃₂₅ and A₄₃₂₆ of 28S rRNA [10]. That is why crotin II is not listed in Table 1. Crotin I is a 40 kDa protein that does not fit into the type 1 RIP classification with regard to the molecular weight and in addition, its \textit{N}-glycosidase activity was also not detected, because the corresponding assay was not performed [273,274]. Thus, the \textit{N}-glycosidase activity cannot be excluded and, therefore, crotin I should be classified as a type 1 RIP candidate. At this point, it should be mentioned that there is a type 1 RIP with \textit{N}-glycosidase activity against bacterial rRNA [277], which was denominated as crotin 2. The denomination of crotin II and crotin 2 may lead to confusion.
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particularly in Girbés et al. [7], as crotin I and crotin II are also denominated as crotin 2 and crotin 3, respectively. For that reference, however, we could not find any proof and, therefore, in Table 1, we listed crotin I and crotin 2 separately, but we did not list crotin II on the basis of the reasons mentioned above and also excluded crotin 3, because too little information exists. The question remains as to whether there are more RIPS which should be demoted.

4. Conclusions

Hitherto, several approaches concerning the nomenclature of RIPS were proposed. Most of the proteins were denominated by using a part of the genus or species name followed with the ending “-in”, e.g., agrostin from *Agrostemma githago* or ocymoidin from *Saponaria ocymoides*. If there is more than one RIP synthesized by the same plant, the denominations are followed by an Arabic or Roman numeral, e.g., asparin 1 and asparin 2 from *Asparagus officinalis* or pulchellin PI, pulchellin PII, and pulchellin PIII from *Abras pulchellus*. The numerals, however, can also represent the peak number, in which the proteins were eluted, e.g., agrostin 2, agrostin 5, and agrostin 6 [112]. Some proteins are denominated with additional information about their molecular weight, e.g., dianthin29 from *Dianthus barbatus* with a size of 29 kDa, or the tissue they are obtained from, e.g., nigrin b from the bark of *Sambucus nigra*. There are also many proteins, which are denominated with abbreviations, mostly using the initials of the genus and species name, e.g., SEA (= *Sambucus ebulus* agglutinin) from *Sambucus ebulus*. At last, modeccin 4B and modeccin 6B from *Adenia digitata* were denominated by using the material for their isolation. Modeccin 4B was isolated by affinity chromatography on Sepharose 4B and modeccin 6B was isolated by affinity chromatography on acid-treated Sepharose 6B [390].

In 1996, an unambiguous nomenclature was already demanded [58], but today there is still not a uniform classification existing for RIPS. This may be due to the fact that there are several exceptions of RIPS and RIP related proteins, which cannot be grouped into the classical type 1 or type 2 RIPS concerning the structure and/or function of these proteins. Besides the small RIPS, which were already designated in 1996 [205], we propose the term “RIP candidate” for those proteins, which are structurally related to the classical type 1 and type 2 RIPS and/or inhibit translation, but were not analyzed with regard to their N-glycosidase activity. On the other hand, ε-momorcharin is also a RIP candidate [203], which is indeed active as *N*-glycosidase but shows significant structural dissimilarities from the classical RIPS. These “RIP candidates” can be subdivided into small type 1 RIP (e.g., cucursenshin), type 1 RIP (e.g., sativin) or type 2 RIP candidates (e.g., malanin) concerning the molecular weight and structure.

For the denomination of those proteins which cannot be grouped into the classic small RIPS, type 1 RIPS or type 2 RIPS due to their unusual structure, but act as *N*-glycosidase (b-32 and JIP60), we agree with the term “peculiar RIP” [7,8], and, therefore, we add the peculiar type 2 RIP foetidissimin, which lacks the disulphide bridge between the A-chain and B-chain. Because of the dimeric structure of panaxagin and quinqueginsin, they should be considered as peculiar type 1 RIPS, or, more precisely, as peculiar type 1 RIP candidates, because the *N*-glycosidase activity could not be analyzed, but they show amino acid sequence similarities with other type 1 RIPS.

All other proteins, which are structurally related to RIPS but lack *N*-glycosidase activity, should be referred to as RIP 1-like or RIP 2-like proteins/lectins.
Author Contributions

J.S. designed and wrote the review. A.W. and M.F.M. designed and proofread the review.

Conflicts of Interest

The authors declare no conflict of interest.

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