

The nitrophilous vegetation of rock shelters on limestone in the Haut-Jura (Ain, France) in a European context

Die nitrophile Vegetation der Kalksteinüberhänge im Hochjura (Ain, Frankreich) im europäischen Kontext

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In memory of our friend Professor Otto Hegg (19.11.1930–03.03.2024)

Abstract

A study of the vegetation of limestone rock shelters in the Haut-Jura has revealed a new specialised association, *Chenopodio boni-henrici-Arabidetum alpinae*. The ecological factors that determine its presence are of zoogenic origin (mammalian resting place), leading to a moderate input of nutrients and an input of diaspores (endozoochory) and a combination of stratigraphic (contact of a soft layer overlaid by a hard layer), petrographic (rock fragments) and geomorphological (export and dispersal of fragments) factors. From a symphytosociological point of view, the association belongs to the described landscape unit of limestone cliffs, which corresponds to a hypogeosigmassociation. A comparison is made with other rock shelter plant communities in Europe. The nomenclature of the names of several syntaxa of the classes *Sisymbrietea sophiae*, *Artemisietea vulgaris*, *Epilobietea angustifolii* and *Mulgedio-Aconitetea* in relation to these communities is reviewed, leading to the validation of the name *Hackelio deflexae-Blitetalia virgati* retained in the EuroVegChecklist, but currently invalid, as well as some lectotypifications.

Keywords: *Arction lappae*, *Chenopodio boni-henrici-Arabidetum alpinae*, *Erysimo witmannii-Hackelio deflexae*, EuroVegChecklist, fauna, *Geo-Alliarion*, geomorphology, geosymphytosociology, Jura, limestone, *Onopordion*, resting place, rock shelter, *Rumicion alpini*, *Sisymbrium officinalis*, stratigraphy

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Cavities at the base of limestone cliffs, or rock shelters (also known as ‘balmes’ or ‘barmes’), have always provided natural shelter. Large rock shelters were used by prehistoric man in the Palaeolithic in the Alps (Praz et al. 2000, Gallay 2008), the Jura (Le Tensorer 1998), the Swabian Jura in southern Germany (Rebholz 1931) and the Carpathians

(Bernátová 1986, Mucina et al. 2016). The small ones, between 2 and 5 m deep and of different sizes and shapes, mainly serve as resting places and refuges for wildlife, especially chamois (*Rupicapra rupicapra* L.), during the off-season (Rübel 1930, Hainard 1988, Schaer et al. 1989) or as observation points. These places, sheltered from precipitation, can host rare and specialised plant species (Bernátová 1987, Bernátová & Škovirová 1988), which are considered to be relics from the end of the last glaciation or the beginning of the Holocene and form unique nitrophilous plant communities (Braun-Blanquet & Sutter 1983, Bernátová 1986, 1991, Bernátová & Obuch 1995, Mucina et al. 2016, Bernátová et al. 2024).

Apart from the work of Richard (1972) in the central Jura, the phytosociological and ecological study of cliffs of the Jura has not been the subject of in-depth studies. Thus, the rock shelters at the foot of the subalpine cliffs in the Jura have not been described in detail, probably because they are little known due to their rarity, but also because they pose classification problems with their nitrophilous vegetation resting on a rocky substratum, far from the vicinity of pasture chalets and livestock resting places.

The aims of this work are (1) to describe the specialised vegetation associated with the particular edaphic complex of rock shelters, taking into account the particular geological and geomorphological setting of the western Jura and reconsidering the classification of previously described plant communities, (2) to place this vegetation in its landscape setting using a simplified symphytosociological method, and (3) to comment on and validate separately, from a nomenclatural point of view, the names of some syntaxa related to nitrophilous vegetation that are part of the EuroVegChecklist (EVC; Mucina et al. 2016).

2. Methods

2.1 Study area

The Jura is a limestone massif, 350 km long and generally north-east-trending, which separates from the Alps at the Grande Chartreuse, north of Grenoble (Isère, France). It culminates in the first anticline north-west of Geneva (Ain, France) at Crêt de la Neige (1720 m a.s.l.) (Supplement E1).

The first comprehensive geological study of the Jura was carried out by the Swiss geologist Jules Thurmann (1832, 1836). Following Thurmann, geologists now consider the Jura to be the reference region for straight, regular folds. The tectonic model is that of a chain of autochthonous folds, more or less eroded. However, as Derruau (1988) puts it: ‘While the central Jura is a chain of regular, uncomplicated folds, the western Jura is a more complicated chain’. In fact, the south-western part of the Jura has been more tectonically active than the north-eastern part. The tectonic activity has created a network of faults and diaclasses, weak points where local glaciers and erosion have cut perpendicularly into the flanks of the anticlines of the straight, regular folds of the Jura chain to form ‘ruz’, namely cataclinal small valley cut into the flank of an anticline (Fig. 1, Supplement E2). The cliffs are the result of the formation of cataclinal ridges and valleys by karstic and periglacial erosion. In the area of Le Reculet, the subvertical cliffs correspond to resistant Portlandian and Kimmeridgian beds resting on less resistant layers of Sequanian and Argovian marl limestone. However, these beds are not petrographically uniform. The Upper Kimmeridgian is a facies with a high proportion of clay and dolomite (false cargneule) of low strength, overlain by a hard Portlandian oolitic layer. Towards the base of the Kimmeridgian, a moderately resistant ‘transitional formation’ (tubular dolomite, false cargneule, pure limestone, micritic limestone with clasts or microbréchiques limestone; Jaquet 1968) underlies a hard and resistant facies with a high calcite content of the Lower Kimmeridgian (Fig. 3). When moving eastwards in the central Jura, this ‘transitional formation’ is absent (Supplement E3). The Sequanian marl-limestone layer is also weaker, which is not conducive to the formation of ruz and steep slopes (drainage system). The geomorphology of the cliffs is also different (anticlinal crests, cirques or

closed basins) (Supplement E2). Our work is concerned with an exceptional case in Le Reculet, namely a Kimmeridgian structural protrusion that has not disappeared under the mantle of debris covering the slope (Fig. 2a and b, Supplement E4).

Geomorphologically, Aubert (1965) divided the Jura into two parts. On the one hand, the ‘rocky Jura’, which extends from Pontarlier to the Ain and Valserine valleys, was covered by the Jura ice sheet during the last glaciation (Würm), which shaped the soil that had previously formed. On the other hand, there is the ‘grassy Jura’, which was not covered by the ice sheet during the last glaciation. Except in places where local glaciers formed, this allowed pre-glacial soils to persist.

Geographically, Thurmann (1849) divided the Jura into four parts: the southern Jura from the Grande Chartreuse to a line between Bellegarde and Bourg-en-Bresse, then the western Jura to a line between Yverdon and Besançon in the north, followed by the central Jura to a line between Solothurn and Belfort, and finally the eastern Jura to the north of this last line (Supplement E1).

Bioclimatically, it is accepted that there is a true subalpine vegetation belt in the Jura (Béguin 1974, Theurillat 1991, Vittoz 1998), which begins at around 1250–1300 m a.s.l. in the Reculet region (western Jura) and at around 1200 m a.s.l. in the Chasseral region (central Jura), due to the shift in elevation with latitude (Ozenda 1985).

2.2 Vegetation relevés

Twelve phytosociological relevés of the ‘*Chenopodietum subalpinum*’ of Béguin (1974), performed during the years 1968–1970 according to the Braun-Blanquet school (Braun-Blanquet 1964) and analysed by Di Maio (2016) were used. Seven of them related to rock shelters were compared with published relevés from the original diagnoses of similar plant communities. Diagnostic taxa of association correspond mainly to regional differential taxa against other associations of rock shelters, and to character and differential taxa for syntaxa at a higher rank.

2.3 Vegetation landscape

The formal analysis of the vegetation landscape (symphytosociology s.l.), initiated about fifty years ago by Tüxen (1973) and subsequently developed mainly by Béguin, Géhu, Hegg and Rivas-Martínez (see Béguin et al. 2016), follows the concepts of Theurillat (1992). Using a simplified method proposed by Béguin (1999), the delimitation and production of sigma-relevés at the catenal level (geosymphytosociology) are carried out directly on a vegetation map, in our case the 1:5000 map produced by Béguin (1974). For each vegetation unit in the relevé, three pieces of information are given: its spatial distribution within the relevé area, its cover and the shape of the unit (mainly punctual, linear or spatial) (see Theurillat 1992, Béguin 1999).

2.4 Taxonomy, syntaxonomy and nomenclature

Taxonomic concept and nomenclature of vascular plants follow Euro+Med 2006+ (Euro+Med PlantBase, <https://euplusmed.org/>) unless otherwise indicated. Phytosociological units above the association rank follow Mucina et al. (2016) or Aeschimann et al. (2004), and associations follow Béguin (1974) and Theurillat & Béguin (1985) where otherwise not indicated. Sociology of taxa follows Aeschimann et al. (2004). Life forms are taken from Landolt et al. (2010). Citation of International Code of Phytosociological Nomenclature (ICPN) articles refers to its fourth edition (Theurillat et al. 2021).

3. Results

The subassociation *arabidetosum alpinae* of the ‘*Chenopodietum subalpinum*’ of Béguin (1974) of the rock shelters of the Haut-Jura corresponds to a new association, the *Chenopodio boni-henrici-Arabidetum alpinae* ass. nov. (see Appendix at the end of the article). The association is dominated by nitrophilous species of the *Artemisietea vulgaris*

(*Chenopodium bonus-henricus*, *Urtica dioica*), accompanied by grassland species (*Galium album*, *Festuca pratensis*, *Dactylis glomerata*). The diagnostic species (Table 1) are mainly scree species of the *Thlaspietea rotundifolii* (*Arabis alpina*, *Rumex scutatus*, *Valeriana montana*, *Scrophularia juratensis*), grassland species (*Pimpinella major*, *Avenula pubescens*, *Silene vulgaris* subsp. *vulgaris*), as well as tall herbs (*Heracleum sphondylium* subsp. *montana*) and woodland species (*Corydalis solida*). Of the total of species (68), a high proportion (24%) are grassland (*Molinio-Arrhenatheretea*) and subalpine-alpine sward species (15%; *Elyno-Seslerietea*, *Juncetea trifidi*), the latter being mainly accidental (Table 1). The plant cover is open (average cover 67%), with no single species dominating, although *Arabis alpina* has the highest cover. Hemicryptophytes are clearly dominant (69%). Therophytes are rather poorly represented (12%), on a par with chamaephytes (12%) and close to geophytes (9%).

The new association is supported in a comparative study of the evolution of the vegetation of Le Reculet by Di Maio (2016). Using the twelve relevés of the ‘*Chenopodietum subalpinum*’ of Béguin (1974), Di Maio highlighted, by means of numerical principal component analyses and using indicator values, the difference between the relevés belonging to the *arabidetosum alpinae* subassociation, and those belonging to the subassociation *typicum* and other recent relevés of resting places. Along a gradient of soil aeration, pH and light in the positive part of axis 1 and humus content, nutrients and light in the negative part, there is a clear difference between the relevés of the *arabidetosum alpinae* subassociation in the rock shelters, all located in the positive part of axis 1, and those of the resting places near the pasture chalets, all grouped in the negative part of axis 2 (Supplement E5).

Table 1. Phytosociological table of the *Chenopodio boni-henrici-Arabidetum alpinae*.

Tabelle 1. Pflanzensoziologische Tabelle des *Chenopodio boni-henrici-Arabidetum alpinae*.

Relevés	1	2	3	4	5	6	Frequency (%)	Plant life form
Relevés Béguin (1974)	R. 7	R. 6	R. 10	R. 9	R. 11	R. 8		
Elevation (m a.s.l.)	1530	1530	1560	1540	1600	1450		
Aspect	E	E	SW	E	E	E		
Slope (°)	10	15	2	2	2	5		
Cover (%)	90	75	50	70	70	50		
Surface of the relevé (m ²)	10	50	10	3	5	5		
Number of species	32	32	31	20	21	14		
Diagnostic species of the association								
<i>Arabis alpina</i>	2.3	2.2	1.2	3.1	1.2	2.2	100	c
<i>Silene vulgaris</i> subsp. <i>vulgaris</i>	+2	1.2	+2	1.2	2.2	.	83	h
<i>Heracleum sphondylium elegans</i> [= <i>H. montanum</i>]	+	1.1	.	r	+	1.1°	83	h
<i>Pimpinella major</i>	+	+	(+)	.	.	.	50	h
<i>Corydalis solida</i>	+	+	r	.	.	.	50	g
<i>Rumex scutatus</i>	+2	(+)	r°	.	.	.	50	h
<i>Avenula pubescens</i>	.	1.1	.	.	+2	+2	50	h
<i>Aconitum anthora</i>	+	+	.	.	.	.	33	h
<i>Scrophularia juratensis</i>	+2	1.2	.	.	.	.	33	h
<i>Valeriana montana</i>	.	1.3	.	.	+2	.	33	h
Diagnostic species of the alliance (<i>Arction lappae</i>), order (<i>Artemisietalia</i>) and class (<i>Artemisietea</i>)								
<i>Chenopodium bonus-henricus</i> (d. all.)	2.2	+	+	1.2	1.1	+2	100	h
<i>Urtica dioica</i> (cl.)	1.2	1.2	+	2.1	r	2.1	100	h
<i>Chaerophyllum aureum</i> (d. all.)	+2	+	.	(+)	.	.	50	h
<i>Geranium robertianum</i> (d. all.)	+	.	1.2	.	.	+	50	t

Relevés	1	2	3	4	5	6	Frequency	Plant
Relevés Béguin (1974)	R. 7	R. 6	R. 10	R. 9	R. 11	R. 8	(%)	life form
<i>Verbascum thapsus</i> (cl.)	.	.	+	.	.	.	17	k-t
<i>Aconitum napellus</i> (d. all.)	.	.	.	.	+	.	17	h
<i>Rumex obtusifolius</i> (all.)	.	.	.	.	.	1.1	17	h
Other species								
<i>Dactylis glomerata</i> (d. all.)	2.1	1.1	(+)	1.2	+	1.2	100	h
<i>Poa alpina</i>	1.2	1.1	1.2	.	.	+	67	h
<i>Galium album</i>	1.2	.	1.2	1.2	+2	.	67	h
<i>Poa angustifolia</i> (d. all.)	1.2	.	1.2	(+)	1.2	.	67	h
<i>Taraxacum officinale</i>	1.1	.	+	(r)	+	.	67	h
<i>Geum montanum</i>	(+)	.	(r)	+	.	r	67	h
<i>Festuca pratensis</i>	.	.	2.2	1.2	1.2	1.2	67	h
<i>Poa supina</i> (d. all.)	.	.	(r)	r	.	+	50	h
<i>Trifolium pratense</i>	+	1.1	+2	.	.	.	50	h-t
<i>Alchemilla vulgaris</i> aggr.	1.1	2.2	.	+2	.	.	50	h
<i>Trisetum flavescens</i>	1.1	1.1	.	+	.	.	50	h
<i>Ranunculus montanus</i>	+	.	+	.	+	.	50	h
<i>Capsella bursa-pastoris</i> (d. all.)	.	.	1.1	.	r	+	50	k-t
<i>Scilla bifolia</i>	2.1	1.1	.	.	.	.	33	g
<i>Rumex acetosa</i>	1.2	1.3	.	.	.	.	33	h
<i>Vicia sepium</i>	+	1.1	.	.	.	.	33	h
<i>Veronica chamaedrys</i>	1.2	+	.	.	.	.	33	c-h
<i>Lathyrus pratensis</i>	+	.	+	.	.	.	33	g
<i>Trifolium repens</i>	.	1.1	+2	.	.	.	33	c-h
<i>Medicago lupulina</i>	.	.	+	+	.	.	33	h-t
<i>Hieracium murorum</i>	.	.	+	.	+	.	33	h
<i>Anthoxanthum alpinum</i>	.	.	+	.	+	.	33	h
Accidental species	5	9	6	4	4	1		

Accidental species occurring in only one relevé. **R. 1:** *Cephalaria alpina* +, *Silene dioica* +, *Phleum rhaeticum* +, *Myosotis alpestris* +, *Centaurea montana* +; **R. 2:** *Geranium sylvaticum* 1.2, *Cardamine pratensis* +, *Digitalis grandiflora* +, *Plantago atrata* +, *Gentiana lutea* +, *Alchemilla conjuncta* +, *Scabiosa lucida* +, *Campanula rotundifolia* +, *Clinopodium alpinum* +; **R. 3:** *Cerastium fontanum* subsp. *vulgare* +, *Senecio vulgaris* +, *Rhinanthus alectorolophus* +, *Veronica hederifolia* +, *Hornungia alpina* +, *Helleborus foetidus* +; **R. 4:** *Galium pumilum* +, *Thymus serpyllum* aggr. +, *Euphorbia cyparissias* +, *Leucanthemum adustum* +; **R. 5:** *Ranunculus platanifolius* +, *Poa nemoralis* +, *Lathyrus vernus* +, *Campanula cochleariifolia* +; **R. 6:** *Epilobium alpestre* (r)

Location and date of the relevés (Béguin, 1974, table 2). **1 (R. 7):** Reculet, above the Creux de Prancio; 1970. **2 (R. 6):** Reculet above the du Creux de Prancio; 1968. **3 (R. 10):** Reculet, Nardaran, under the Voûtes; 1970. **4 (R. 9):** Reculet, above the Creux de Prancio; 1969. **5 (R. 11):** Reculet, Nardaran, ~250 m E pt. 1692; 1969. **6 (R. 8):** Reculet, Creux de Prancio; 1970.

3.1 Synecology

The *Chenopodio-Arabidetum* is a subalpine association. Its presence is linked to the combination of two fundamental factors that allow the formation of a rock shelter: on the one hand, a specific combination of tectonic, stratigraphic, petrographic, geomorphological and climatic factors (see chapter 2.1), and on the other hand, a nitrophilic factor. Rock shelters form naturally at the contact between a more clayey, highly geliferous geological layer and a layer of compact, less geliferous rock above it, with the highly geliferous layer eroding more rapidly, when three fundamental elements are combined: (a) a significant stratigraphic 'transitional formation' that allowed the shelter to form, (b) a thick layer of marl-limestone overdeepened by the local glaciers, and (c) a steep slope below the rock shelter to allow the weathering material that has fallen from the roof to be drained away. At Le Reculet,

well-developed and well-preserved rock shelters have formed without fillings in the less resistant Lower Kimmeridgian ‘transitional formation’ (false cargneule), with the underlying hard and resistant facies forming the base of the rock shelter on which the *Chenopodio-Arabidetum* develops (Fig. 2–3). Below the rock shelter, there is a large, steep, concave slope formed by soft Sequanian limestone up to 200 m high, whose vegetation often corresponds to open grasslands of the *Campanulo-Laserpitietum*, *Laserpitio-Calamagrostietum* (*Caricion ferruginae*) or *Seslerio-Laserpitietum* (*Seslerion caeruleae*) (Fig. 1 and 2a, b). This location allows the material from the erosion zone and the overlying hard oolitic limestone layer to be effectively removed by gravity. In this way, input is approximately equal to output. The accumulated boulders are slowly transported to the edge of the rock shelter by the effects of climatic hazards (freeze-thaw, creep, concentrated runoff, wind).

The second ecological factor that determines the presence of the *Chenopodio-Arabidetum* is the moderate supply of nitrogen at the flat base of the rock shelter, the main source of which is the excrement of herds of chamois and, less frequently, sheep, ibex and heifers. These deposits are not evenly distributed over thoroughfares and resting areas. Their moderate quantity is reflected in the abundance-dominance of nitrophilous species, whose cover does not exceed 50% and can be very low (Fig. 2a and b). The same is true for species reflecting trampling (*Capsella bursa-pastoris*, *Trifolium repens*, *Medicago lupulina* and *Poa supina*).

The *Chenopodio-Arabidetum* is therefore the result of a combination of alteration processes in a specific geological context, allowing the formation of rock shelters, combined with the necessary nitrogen supply and sufficient trampling.



Fig. 1. General view of the southern slope of the deep ruz de Nardaran (Recullet region). The rock shelters are located at the foot of the cliffs of the two ‘Voûtes’. (Photo: L. Béguin, 16.07.2024).

Abb. 1. Gesamtansicht des Südhangs der Ruz de Nardaran (Region Reculet). Die Felsüberhänge befinden sich am Fuße der Klippen der beiden ‘Voûtes’ (Aufwölbungen) (Foto: L. Béguin, 16.07.2024).



Fig. 2. a) General physiognomy of the rock shelters at the foot of ‘Les Voûtes’ of the ruz de Nardaran (Le Reculet, western Jura). Overdeepening of the ‘transitional formation’ with the Kimmeridgian structural terrace, where some alteration materials have been deposited and colonised by the weakly nitrophilous vegetation of *Chenopodio boni-henrici-Arabidetum alpinae*. **b)** Rock shelter and its Lower Kimmeridgian structural terrace on which the *Chenopodio-Arabidetum alpinae* developed (Le Reculet, western Jura). The granulometric sorting that takes place from the inside to the outside is clearly visible, resulting in a tendency towards fine scree vegetation (*Stipion calamagrostis* = *Scrophularion juratensis*) inside the shelter, while the coarser external debris harbours vegetation tending towards the *Arabidion alpinae* (Photos: L. Béguin, 16.07.2024).

Abb. 2. a) Allgemeine Physiognomie der Felsüberhänge am Fuße der Aufwölbungen des Ruz de Nardaran (Le Reculet, Westjura). Übertiefung der ‘Übergangsformation’ zur Strukturterrasse des Kimmeridgiums, wo einige Sekundärmaterialien abgelagert und von der schwach nitrophilen Vegetation des *Chenopodio boni-henrici-Arabidetum alpinae* besiedelt wurden. **b)** Felsüberhang und seine Strukturterrasse des Unteren Kimmeridgiums, auf der sich das *Chenopodio-Arabidetum alpinae* entwickelt hat (Le Reculet, Westjura). Die von innen nach außen stattfindende granulometrische Sortierung ist deutlich erkennbar. Im Inneren des Überhangs tendiert die Vegetation zu feinem Geröll (*Stipion calamagrostis* = *Scrophularion juratensis*), während das gröbere Schuttgestein außen eine zum *Arabidion alpinae* tendierende Vegetation beherbergt (Fotos: L. Béguin, 16.07.2024).

3.2 Vegetal landscape (geosymphytosociology)

From a landscape point of view, the *Chenopodio-Arabidetum* belongs to the limestone cliff complex, which therefore includes the base of the niche (Fig. 2b and 3) of the rock shelter, which corresponds to the base of the cliff complex. The cliff forms a catenal unit of the hypogeosigmassociation level (Theurillat 1992; microgeosigmassociation sensu Rivas-Martínez 1994). This landscape unit follows the previously described landscape units (Béguin 1996, 1999, Béguin et al. 2023). Although for practical reasons (difficulty of access, scale of the 1:5000 map) it was not possible to map the exact position of the different plant

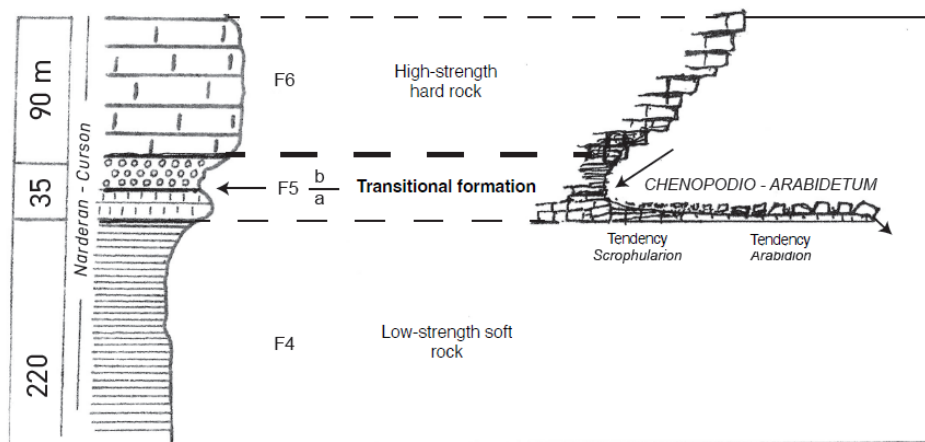


Fig. 3. Semi-schematic profile of a rock shelter in the western Jura (Nardaran, Reculet). The arrow indicates the position of the *Chenopodio-Arabidetum alpinae* in the 'transitional formation' between the Lower Kimmeridgian facies F5a and F5b. The gelifraction material is unevenly distributed across the terrace, with the *Chenopodio-Arabidetum alpinae* tending towards a fine scree vegetation (*Stipion calamagrostis* = *Scrophularion juratensis*) inside the shelter, while the coarser outer debris pile supports a vegetation tending towards the *Arabidion alpinae* (see Fig. 2a and b, Supplement E4).

Abb. 3. Halbschematisches Profil eines Felsüberhangs im westlichen Jura (Nardaran, Reculet). Der Pfeil zeigt die Position des *Chenopodio-Arabidetum alpinae* in der 'Übergangsformation' zwischen den Fazies F5a und F5b des Unteren Kimmeridgiums. Das Frostsprengungsmaterial ist ungleichmäßig über die Terrasse verteilt, wobei das *Chenopodio-Arabidetum alpinae* innerhalb des Überhangs zu einer feinen Geröllvegetation (*Stipion calamagrostis* = *Scrophularion juratensis*) tendiert, während der größere äußere Schutthaufen eine zum *Arabidion alpinae* tendierende Vegetation trägt (siehe Abb. 2 und 3, Anhang E4).

communities of the cliff, we can formally describe the hypogeosigmassociation of the subvertical limestone cliffs, the *Potentillo caulescentis-Hieracieto humilis*-hypogeosigmatum (Table 2, sigmarelevé type: relevé 1), which is a primary montane-subalpine unit composed of (a) rock fissure associations (*Potentillo caulescentis-Hieracietum humilis*, *Moehringio muscoidis-Asplenietum viridis*, *Androsaco lacteae-Ranunculetum alpestris*, accompanied by undefined bryolichenic plant communities), (b) the swards on the slopes and flats, and (c) the base of the rock shelters at the foot of the cliffs (*Chenopodieto-Arabidetum*) where they exist. Two sub-units (sub-hypogeosigmassociations) can be distinguished, one with the presence of rock shelters and the other without, i.e. where the base of the cliff is filled in. Only the first sub-unit is described here, which is the typical sub-hypogeosigmassociation, whose differential unit is the *Chenopodio-Arabidetum*. It can be subdivided into a dry facies (Table 2, r. 1 and 2) and a wet facies (Table 2, r. 3–5) the later with *Cystopteridion fragilis* associations (*Moehringio muscoidis-Asplenietum viridis*, *Androsaco lacteae-Ranunculetum alpestris*), an alliance that was not yet distinguished when the vegetation map was drawn up.

This landscape has been little affected by man. The anthropogenic impact is therefore very limited; the effect of climbers is negligible. It is locally limited to a footpath at the foot of the cliff (Supplement E4). On the scale of 0 to 10 developed by Géhu & Géhu (1981), the degree of artificiality is 1. According to the phytosociological map and our field

Table 2. Simplified symphytosociological relevés of the vegetation landscape of the meso-thermophilous calcareous cliffs with rock shelters (*Potentillo caulescentis*-*Hieracieto humilis*-hypogeosigmatum).

Tabelle 2. Vereinfachte synsoziologische Aufnahmen der Vegetationslandschaft der meso-thermophilen Kalkfelsen mit Felsüberdachungen (*Potentillo caulescentis*-*Hieracieto humilis*-Hypogeosigmatum).

Relevé number	Dry facies		Humid facies			Frequency (%)
	1	2	3	4	5	
Mean elevation (m a.s.l.)	1450	1590	1540	1400	1540	
Mean slope (°)	70	75	70	70	65	
General aspect	SO	SO	NE	NE	NNE	
Surface (a)	20	20	15	10	20	
Number of associations/ sigmarelevé	6	5	5	5	5	
Characteristic combination of associations						
<i>Potentillion caulescentis</i> [26] [incl. <i>Potentillo caulescentis</i> - <i>Hieracietum humilis</i> , <i>Moehringio muscoidis</i> - <i>Asplenietum viridis</i> , <i>Androsaco lacteae</i> - <i>Ranunculetum alpestris</i>]	/ 3 2	/ 3 2	/ 3 2	/ 3 2	/ 3 2	100
Bryo-lichenic communities						
<i>Chenopodio-Arabadetum alpinae</i>	O 3 4	O 3 4	O 3 4	O 3 4	O 3 4	100
<i>Seslerio-Arctostaphyletum</i> [1]	/ 1 2	/ 1 2	/ 1 2	/ 1 2	/ 1 2	100
<i>Campanulo-Laserpitietum</i> [10]	/ 1 3	/ 1 3	/ 1 3	/ 1 3		80
<i>Seslerio-Laserpitietum</i> [2]	/+3	/+3				40
<i>Laserpitio-Calamagrostietum</i> [11]	°r3					20
<i>Sorbo-Aceretum</i> [22]			/ 1 3			20
<i>Pulsatillo-Anemonetum rhododendretosum</i> [13]				/ 1 3		20
					/+3	20

Location of the sigma-relevés according to the vegetation map 1: 5000 Reculet - Crêt de la Neige (Béguin 1974).

Relevé 1. Lower and upper 'Les Voûtes'. Relevé 2. Upper 'Les Voûtes'. Relevé 3. Upper 'Prancio'.

Relevé 4. Lower 'Prancio'. Relevé 5. 'Sur Thoiry'.

[]: unit number according to the vegetation map

Symphytosociological information in the relevé. First indication: shape of the unit (/ = linear, O = spatial). Second indication: cover ($r < 0.1\%$, + = $< 1\%$, 1 = 1–5%, 3 = 25–50%). Third indication: spatial distribution within the relevé (2 = > 5 isolated occurrences as a mosaic, 3 = isolated but concentrated occurrences (edge, center, extremity), 4 = linked occurrences forming a kind of weft)

observations, the landscape unit of rocky cliffs with rock shelters comes into contact with the plant associations of *Seslerio-Laserpitietum* (*Seslerion caeruleae*) and *Campanulo-Laserpitietum* (*Caricion ferruginae*) on south-western exposures, and *Pulsatillo-Anemonetum rhododendretosum* (*Caricion ferruginae*) on the northeast exposure.

The sub-hypogeosigmassociation of *Potentillo caulescentis*-*Hieracieto humilis*-hypogeosigmatum *typicum* is part of the large, well-defined geomorphological complex of the Ruz or Creux de Nardaran (Fig. 1). Its physiognomy contrasts with the sigmassociations in contact, which are located on slopes following the dip of the bedding (structural sigmassociations), namely the *Plantagini-Cariceto*-sigmetum and the *Seslerio-Arctostaphyleto*-sigmetum, to the south and north respectively, and the *Valeriano-Rhamneto*-sigmetum and the *Seslerio-Cariceto bupleureto*-sigmetum, to the east and west respectively of the Creux de Nardaran. The latter (Fig. 1), with an area of more than 10 hectares, is the largest and most beautiful ruz in the Jura, offering a remarkable and unique wealth of landscapes.

4. Discussion

4.1 The *Chenopodio boni-henrici-Arabidetum alpinae*, a specificity of the western Jura

As one moves from the ‘rocky’ Jura to the ‘grassy’ Jura, rock shelters become rarer and less well developed because the ‘transitional formation’ at the base of the Kimmeridgian (hardrock) is absent (see chapter 2.1). As a result, we no longer find the three fundamental elements associated with rock shelters in the Reculet region (see chapter 3.1). The inflow being greater than the outflow, the rock shelters are more or less filled in by debris from periglacial erosion of the rock face, which accumulates on the slope, leading to their partial filling. They are filled all the more quickly when excavation is less effective because the contrast in resistance between hard rock and soft rock is not very marked. The rock shelters are then almost invisible due to the structure of the cliff (Supplements E6 and E7). In the particular case of the Creux du Van in the central Jura, the overlying cliffs are very high and overflowing, with landslides (Supplement E6). The foot of the large cliffs has been covered by partially vegetated scree or even forest. Therefore, the vegetation is different from the *Chenopodio boni-henrici-Arabidetum alpinae*, with more or less woodland species (*Adenostyles glabra*, *Helleborus foetidus*, *Mercurialis perennis*, *Knautia silvatica*) and species with a certain degree of hardiness (*Senecio viscosus*, *Senecio vulgaris*, *Cynoglossum germanicum*, *Fumaria vaillantii*) (see chapter 4.3).

4.2 Syntaxonomy of the *Chenopodio boni-henrici-Arabidetum alpinae*

The plant community of the *Chenopodio-Arabidetum*, far from the pasture chalets and overdunged resting places, has always posed classification problems. Thus, during the revision of the *Rumicion alpini* alliance as part of the Phytosuisse project (Prunier et al. 2014), the question arose as to the status of the subassociation of rock shelters ‘*arabidetosum alpinae* (Béguin 1974) Theurillat et Béguin 1985’ of the ‘*Cynoglossos germanici-Alliarietum petiolatae* Géhu, Richard et Tüxen ex Theurillat in Theurillat et Béguin 1985 nom. invers.’ (= ‘*Chenopodietum subalpinum arabidetosum* Béguin 1974’; see Appendix). Shouldn't this subassociation have been raised to the level of an association, as Béguin already suggested in 1974, instead of being kept within the *Cynoglossos-Alliarietum* due to the existence of transitional stages with the lowland subassociation (Theurillat & Béguin 1985)?

Despite the importance of the meadow and scree diagnostic species, the *Chenopodio-Arabidetum* should be placed in the nitrophilous class of *Artemisietea vulgaris*, due to the constant presence of *Urtica dioica* and *Chenopodium bonus-henricus*, which have a fairly high proportional cover. The association is therefore mainly a more or less nitrophilous community on a rocky substrate. As far as the alliance is concerned, the association leans more towards the *Arction lappae* than the tall herbs (*Rumicion alpini*, *Senecioni rupestris-Rumicetalia alpini*; see Appendix), considering the constancy of *Chenopodium bonus-henricus*, the absence of *Rumicion species* and the fact that the few differential species of the *Mulgedio-Aconitetea* are mainly accidental. In fact, the *Rumicion alpini* is absent from the Jura (Preislerová et al. 2022) because several of the good diagnostic species of this alliance are absent (*Cirsium spinosissimum*, *Peucedanum ostruthium*, *Senecio alpinus*) or rare (*Cerinth glabra*, *Rumex alpinus*, *Senecio rupestris*). The order is that of the *Artemisietalia vulgaris* (see Appendix).

4.3 Associations close to the *Chenopodio-Arabidetum*

The first mention of a provisional 'association with *Cynoglossum germanicum* and *Alliaria petiolata*' was made by Géhu et al. (1972 p. 15) for rock shelters in Creux du Van (central Jura). Korneck (1974 p. 144) mentioned the plant community '*Cynoglossum germanicum*-Gesellschaft' in Germany in the Rhineland-Palatinate (Donnersberg) for forest resting places. Müller (1983 p. 194) raised Korneck's *Cynoglossum germanicum* plant community to the rank of an association and gave it the name proposed by Géhu et al. (1972), but without retaining the latter's relevés and without indicating a type relevé. In 1974, Béguin described a new subassociation '*arabidetosum alpinae*' within the *Chenopodietum subalpinum* Braun-Blanquet 1950 for rock shelters in the Haut-Jura (Reculet, Ain, France), together with a relevé from the Creux du Van. In an inventory of the plant communities of the canton of Neuchâtel (Jura, Switzerland), Theurillat & Béguin (1985) validated Müller's name '*Alliario petiolatae-Cynoglossetum germanici*' and, by including the subassociation '*Chenopodietum subalpinum arabidetosum alpinae* Béguin 1974', subdivided the association into two new subassociations, namely (1) '*alliarietosum petiolatae*' [recte: *typicum*] and (2) '*arabidetosum alpinae*'. Despite their preference for a single association, the authors remained cautious, stating that 'one might think that we are dealing with two associations rather than two subassociations'.

The separation of the *Chenopodio-Arabidetum* from the resting places of the '*Chenopodietum subalpinum*' [recte: *Urtico dioicae-Chenopodietum boni-henrici* (Braun-Blanquet 1950) Rivas-Martínez et Géhu 1978; see Appendix] is justified from a floristic point of view by the absence of diagnostic species of the first association (*Arabis alpina*, *Rumex scutatus*, *Scrophularia juratensis*, *Valeriana montana*) within the second and by the absence or low presence in the *Chenopodietum subalpinum* of *Festuca pratensis*, *Galium album*, as well as *Geranium robertianum* and, conversely, the presence in the *Chenopodietum subalpinum* of nitrophilous species (*Galeopsis tetrahit*, *Cirsium eriophorum*, *Veronica serpyllifolia* subsp. *humifusa*) and ruderals as *Daucus carota*, which are absent from rock shelters (Supplement E8). The subassociation *typicum* of the *Chenopodietum subalpinum* sensu Béguin (1974) differs from the *Chenopodietum subalpinum* of the Alps and the provisional *Alchemillo-Chenopodietum boni-henrici* proposed by Géhu et al. (1972) for the central Jura (see *Cirsium eriophorum-Rumex obtusifolius* community; Supplements E5 and E8).

The transfer of the subassociation *arabidetosum alliariae* from the *Chenopodietum subalpinum* (Béguin 1974) to the *Cynoglossum germanici-Alliarietum petiolatae* by Theurillat & Béguin (1985) was based on the existence of intermediate situations of the provisional association with *Cynoglossum germanicum* and *Alliaria officinalis* described by Géhu et al. (1972), despite the few common species and the presence of numerous differentials. However, the montane relevés from Rhineland-Palatinate (Germany; Korneck 1974) of the *Cynoglossum germanici-Alliarietum petiolatae* differ from the subalpine relevés of Le Reculet in that they clearly belong to the *Geo-Alliarion petiolatae* and not to the *Arction*, with therophytes besides *Alliaria petiolata* and *Cynoglossum germanicum* such as *Galium aparine*, *Chaerophyllum temulum* and *Lapsana communis*, as well as the scarce presence of grassland species from the *Molinio-Arrhenatheretea*, which are replaced by forest species, mainly from the *Carpino-Fagetum sylvaticae* class (*Mercurialis perennis*, *Stellaria holostea*, *Melica uniflora*; Supplement E8). Regarding the provisional intermediate association with *Cynoglossum germanicum* and *Alliaria officinalis* of Géhu et al. (1972) for the rock shelters of the central Jura filled in by weathering deposits, it belongs to the *Cynoglossum-Alliarietum*

and not to the *Chenopodio-Arabidetum*, despite the presence of *Arabis alpina*, *Rumex scutatus* and *Corydalis solida*, but with the presence of *Cynoglossum germanicum*, *Alliaria petiolata*, *Galium aparine*, *Mercurialis perennis* and several differential species such as *Fumaria vaillantii*, *Senecio viscosus*, *Geranium robertianum*. Together with *Epilobium montanum*, these species give the Jura relevés the status of a new subassociation *fumarietosum vaillantii* of the *Cynoglosso-Alliarietum* (Appendix, Supplement E8).

Smettan (1981) described a provisional association *Cynoglosso germanici-Chenopodietum boni-henrici* on the basis of two relevés. This association was later validly published by Mucina (1993). The site was a resting place in the Kaisertal (Tirol, Austria), located at the foot of a limestone wall in the subalpine zone, and corresponding exactly to the *Chenopodio-Arabidetum* of the Jura. Smettan attributes the association to *Rumicion alpini*, whereas Mucina classifies it as *Erysimo witmannii-Hackelion*. However, we classify it as *Arction lappae* (Supplement E8).

When the rock shelter is very pronounced and protected from precipitation, the vegetation of the resting places is characterised by xerophilous nitrophilous therophytes (Rübel 1930) belonging to the class *Sisymbrietea*. This is the case, for example, of the '*Lappulo-Asperuginetum procumbentis*', particularly in the Grisons (Alps, Switzerland) (Braun-Blanquet 1919, 1949, 1976, Braun-Blanquet & Sutter 1983). This invalidly published name is validated as *Lappulo squarrosae-Asperuginetum procumbentis* (Appendix). Braun-Blanquet (1976) classifies this association in an alliance close to *Arction lappae*, the *Arction alpestre*, described as a vicariant of the former for the ruderal nitrophilous vegetation of resting places and rock shelters in the upper montane and subalpine levels of the inner valleys and southern slopes of the Alps (Appendix). A vicariant association, the *Sisymbrio austriaci-Asperuginetum procumbentis*, has also been described in the rock shelters of the Danube valley in Swabian Jura in southern Germany (Rebholz 1931, Oberdorfer 1957) (see Appendix). On the basis of two relevés, Westhoff et al. (1983) described a plant community with *Asperugo procumbens* in rock shelters at the foot of the coastal limestone cliffs of the small island of Stora Karlsö, west of Gotland (Sweden), where the soil is enriched by the guano of seabirds nesting on the cliffs.

In Braun-Blanquet & Sutter (1983), the *Lappulo-Asperuginetum* was divided into a variant with *Asperugo* (eight relevés) and a variant with *Lappula deflexa* (= *Hackelia deflexa*) without *A. procumbens* (five relevés). In the latter variant, the only three relevés containing *H. deflexa* are not from rock shelters but from resting places in the forest. As they differ from the ten other relevés from the rock shelters of several other species, they could form a separate association with *Cirsium arvensis* and *H. deflexa* (*Cirsium arvensis-Hackelia deflexa* community, Supplement E8).

Several associations and subassociations of rock shelters have also been described from the montane belt of the Western Carpathians (Veľká Fatra, Chočské vrchy) in Slovakia (Bernátová 1986, 1991, Bernátová & Obuch 1991, 1995), including the *Hackelio deflexae-Chenopodietum foliosi* Bernátová 1986, *Arenario serpyllifoliae-Descurainietum sophiae* Bernátová 1991, *Taraxaco laevigati-Sisymbrietum austriaci* Bernátová 1991, *Poa nemoralis-Hackelietum deflexae* Bernátová 1991, *Arabido turritae-Sisymbrietum strictissimi* Bernátová 1991 and *Cortuso matthioli-Papaveretum tatrici* Bernátová 1991 (Supplement E8).

4.4 Higher units

According to Mucina et al. (2016), the ‘therophyte-rich zoogenic vegetation of mammal lairs under stone overhangs in the mountains of Central Europe’ belongs to the *Erysimo witmannii-Hackelion deflexae* alliance. Considering the prehistoric relict nature and singularity of this type of vegetation, Mucina (in Mucina et al. 2016) created a new order ‘*Hackelio deflexae-Blitetalia foliosi*’ [recte: *Hackelio deflexae-Blitetalia virgati*] (see Appendix) within the class *Sisymbrietea* to group together this type of vegetation in the mountains of Europe, the Middle East, Central Asia and southern Africa. According to Preislerová et al. (2022), in Europe the alliance is found in Slovakia, Germany, the Alps of Austria, Germany, Italy, Switzerland and France; it is uncertain in the Swiss Jura.

The study of the type of alliance, the *Hackelio deflexae-Chenopodietum foliosi* (Bernátová 1986), and that of the original diagnoses of five other associations in Slovakia attributed to the alliance (Bernátová 1991, see chapter 4.3) show a remarkable floristic and sociological homogeneity at the alliance level (Supplements S1 and E8), with a large number of diagnostic species, in particular *Hackelia deflexa*, *Erysimum witmannii*, *Cicerbita muralis*, *Campanula rapunculoides*, *Taraxacum laevigatum*, *Arabidopsis arenosa*, *Hieracium bifidum* and *Campanula cochleariifolia*, present in all six associations, fully justifying the individuality of the alliance in relation to the syntaxa richer in therophytes and short-lived species like the *Sisymbrium officinalis*, and to some extent also the *Geo-Alliarion* and the *Arction lappae*. In comparison, rock shelter associations in other regions show significant differences in floristic composition, but also in the sociological spectrum and life forms (Supplements S1 and S2). The associations of the *Erysimo-Hackelion* are characterised by a much higher proportion of *Festuco-Brometea*, *Trifolio-Geranietea*, *Asplenietea trichomanis*, *Elyno-Seslerietea* and *Crataego-Prunetea* species. In terms of life forms, the proportion of nanophanerophytes and phanerophytes is remarkable.

Although Mucina (1993: 177) placed the *Cynoglosso-Chenopodietum boni-henrici* of Tyrol in the *Erysimo-Hackelion*, the diagnostic species of this alliance are not found in this association, nor in its western Jura vicariant, the *Chenopodio-Arabidetum alpinae*. These two associations can easily be placed in the *Arction lappae* alliance and the *Artemisietea vulgaris* class with *Chenopodium bonus-henricus*. Their floristic composition is similar to that of the other resting places of the *Arction*. They seem to differ from the latter by the absence of *Polygono-Poetea annuae* species, in particular *Poa annua*, *Polygonum aviculare* and *Plantago major*, as well as *Galeopsis tetrahit* (Supplements S1 and E8). They show that the *Arction lappae* also includes non-anthropogenic semi-natural plant communities and, together with the resting places of the *Urtico-Chenopodietum boni-henrici*, that this alliance extends well into the subalpine level, which is not indicated in Preislerová et al. (2024).

The classification of the *Cynoglosso germanici-Alliarietum petiolatae* of Germany and its subassociation *fumarietosum vaillantii* of the rock shelters of the central Jura within the *Geo-Alliarion* alliance and the *Epilobietea angustifoliae* class also poses no problems, especially with the presence of *Alliaria petiolata*, *Cynoglossum germanicum* and *Galium aparine*. The relative proportion of *Galio-Alliarietalia* and *Carpino-Fagetea* species is higher than in the *Arction* plant communities (Supplements S1 and E8). On the other hand, the relative proportions of the life forms are of the same order of magnitude (Supplement S2). Although not indicated in Preislerová et al. (2024), the Jura rock shelters show that the *Geo-Alliarion* reaches the montane level and that it also includes non-anthropogenic semi-natural plant communities.

According to Mucina (1993: 176), the rock shelters of the *Lappulo-Asperuginetum* (according to the bibliographical references given by the author: Braun-Blanquet 1919, Lüdi 1921, Gams 1927, Braun-Blanquet & Sutter 1983), are also assigned to the *Erysimo-Hackelion deflexae*. A comparison of the relevés of Braun-Blanquet & Sutter (1983) from Graubünden with the Slovakian associations effectively shows some floristic relationship, with *Campanula rapunculoides*, *Taraxacum laevigatum* and *Galium spurium* present in some *Lappulo-Asperuginetum* relevés, and *Descurainia sophia* and *Blitum virgatum*, two species of the *Sisymbrietea*, present in some Slovakian associations (Supplement E8). However, there are significant differences, which is strongly noticeable when comparing the sociological and life form spectra (Supplements S1 and S2). Moreover, the Graubünden relevés count a total of 32 species, whereas the total number of species in the Slovakian associations ranges from 66 to 120. On the sociological level, the proportions of species from the *Artemisietea/Artemisietalia vulgaris*, *Onopordetalia acanthii*, *Agropyretalia intermedii-repentis*, *Sisymbrietea* and *Stellarietea mediae* are significantly higher in the *Lappulo-Asperuginetum* (59% vs. 6–18%), whereas species from the *Festuco-Brometea*, *Trifolio-Geranietea*, *Elyno-Seslerietea*, *Asplenietea trichomanis* and *Carpino-Fagetea* are practically absent, although they represent between 48 and 62% of the floristic composition of Slovakian associations (Supplement S1). In terms of life forms, over 50% of *Lappulo-Asperuginetum* species are therophytes, compared to only 9–22% in Slovakian associations (Supplement S2). This shows that the *Lappulo squarrosae-Asperuginetum procumbentis* is clearly more an association of *Sisymbrium officinalis* than of *Erysimo-Hackelion*. As Braun-Blanquet's relevés range from 1100 to 2070 m a.s.l., they show that the *Sisymbrium officinalis* also includes non-anthropogenic semi-natural plant communities and that it extends into the subalpine zone, which is not indicated in Preislerová et al. (2024).

Despite the presence of *Hackelia deflexa*, *Campanula rapunculoides* and *Blitum virgatum*, the same observations about the overall floristic composition, the sociological spectrum and the spectrum of life forms can be made for the three *Lappulo-Asperuginetum* relevés that are not rock shelters but forest resting places (*Cirsium arvensis-Hackelia deflexa* community). The *Asperugo procumbens* community of Stora Karlsö west of Gotland is also a *Sisymbrium* association in terms of overall floristic composition, sociological spectrum and biological forms (Supplements S1, S2 and E8).

5. Conclusion

The *Chenopodio boni-henrici-Arabidetum alpinae* is a new, specialised plant association that contributes to the high level of biodiversity (flora, vegetation and vegetation landscape) of the Haut-Jura. This plant community does not appear to be threatened by any significant change in anthropogenic activity and therefore does not require special protection. This new association reinforces the thesis of the phytosociological and ecological uniqueness of the Reculet-Crêt de la Neige chain and the role of edaphic factors (geology, geomorphology and pedology) in determining the vegetation.

Depending on the humidity and temperature (vegetation belt) of the substrate, limestone rock shelters can support very different types of nitrophilous vegetation. On the one hand, plant communities of *Artemisietalia vulgaris* (*Artemisietea vulgaris*) and *Galio-Alliarietalia* (*Epilobietea angustifolii*), when the substrate still receives sufficient moisture in a cool climate, and on the other hand, *Sisymbrietalia sophiae* and *Hackelio deflexae-Blitetalia virgati* (*Sisymbrietea officinalis*) when conditions are drier in a warmer climate.

6. Synsystematic scheme

The synsystematic scheme summarises the syntaxonomic position of the rock shelter plant communities discussed in this paper, as well as some close syntaxa mentioned or included in Supplements S1, S2 and E8. These plant communities fall into four classes based on the EuroVegChecklist (EVC). The main divergence from the EVC classification concerns the position of *Arction lappae*. For this syntaxon, we have opted for the alternative position mentioned in the EVC, i.e. to keep this alliance in the class *Artemisietea vulgaris* instead of including it in the class *Epilobietea angustifolii*. The numbering of the EVC is used to avoid any ambiguity in a comparison with the synsystematic position of the EVC.

SIS *Sisymbrietea* Gutte et Hilbig 1975

SIS-01 *Sisymbrietalia sophiae* J. Tüxen ex Görs 1966 nom. cons. propos.

Syn.: SIS-01 *Chenopodio-Urticetalia* Libbert 1932 nom. rejic. propos.

SIS-01D *Sisymbrium officinalis* Tüxen, Lohmeyer et Preising ex von Rochow 1951

Syn.: ART-01A *Hordeo-Onopordion* Libbert 1932 nom. rejic. propos.

Sisymbrio austriaci-Asperuginetum procumbentis Rebholz ex Oberdorfer 1957

Syn.: *Lappulo-Asperuginetum* Braun-Blanquet ex Rebholz 1931 (Art. 3f)

Syn.: *Sisymbrium austriacum-reiche-Lappula-Asperugo*-Assoziation Rebholz 1931

(Art. 3f, 34c)

Lappulo squarrosae-Asperuginetum procumbentis Braun-Blanquet ex Theurillat et Béguin ass. nov.

Syn.: *Lappulo-Asperuginetum procumbentis* Braun-Blanquet 1919 (Art. 2b)

Asperugo procumbens-Gesellschaft Westhof et al. 1983.

Cirsium arvensis-Hackelia deflexa community.

Syn.: *Lappulo-Asperuginetum procumbentis* var. *Lappula deflexa* Braun-Blanquet et Sutter 1983

SIS-02 *Hackelio deflexae-Blitetalia virgati* Mucina et Theurillat ord. nov.

Syn.: SIS-02 *Hackelio deflexae-Blitetalia foliosi* Mucina 2016 in Mucina, Bültmann, Dierssen, Theurillat, Raus et al. 2016 (Art. 3l)

SIS-02A *Erysimo wittmannii-Hackelion deflexae* Bernátová 1986 [holotype of the order]

Hackelio deflexae-Chenopodietum foliosi Bernátová 1986 [holotype of the alliance]

ART *Artemisietea vulgaris* Lohmeyer, Preising et Tüxen ex Pignatti 1952

Syn.: *Artemisietea vulgaris* Lohmeyer, Preising et Tüxen ex von Rochow 1951 (Art. 2b)

ART-01 *Onopordetalia acanthii* Braun-Blanquet et Tüxen ex Klika in Klika et Hadač 1944 (typus cons. propos.)

Syn.: ART-01 *Onopordetalia* Braun-Blanquet et Tüxen 1943 (Art. 2b)

ART-01A *Onopordion acanthii* Braun-Blanquet in Braun-Blanquet, Gajewski, Wraber et Walas 1936

Syn.: ART-01A *Onopordion* Braun-Blanquet 1926 (Art. 2b)

Syn.: ART-01A *Onopordion* Braun-Blanquet ex Klika in Klika et Novák 1941 (Art. 3l)

Onopordetum acanthii Braun-Blanquet in Braun-Blanquet, Gajewski, Wraber et Walas 1936 nom. cons. propos.

Syn.: *Onopordetum acanthii* Libbert 1932

EPI-03 *Artemisietalia* Tüxen 1947

Syn.: EPI-03 *Arctio lappae-Artemisietalia vulgaris* Dengler 2002 (Art. 29c)

EPI-03A *Arction lappae* Tüxen 1937

Syn.: MUL-04A *Chenopodion subalpinum* Braun-Blanquet 1949

[not in the EVC] *Arction alpestre* Braun-Blanquet 1976

Chenopodio boni-henrici-Arabidetum alpinae (Béguin 1974) Béguin ass. nov. et stat. nov.

Nom. corresp.: *Chenopodietum subalpinum arabidetosum alpinae* Béguin 1974

Cynoglosso germanici-Alliarietum petiolatae arabidetosum alpinae Theurillat et Béguin 1985

Urtico dioicae-Chenopodietum boni-henrici (Braun-Blanquet 1950) Rivas-

Martínez et Géhu 1978

Syn.: *Chenopodietum subalpinum* Braun-Blanquet 1950 (Art. 34)

Alchemillo-Chenopodietum boni-henrici Géhu, Richard et Tüxen 1972 (Art. 2b)

Cynoglosso officinalis-Chenopodietum boni-henrici Smettan ex Mucina 1993

Cirsium eriophorum-Rumex obtusifolius community (Supplements E5, E8)

Nom. corresp.: *Chenopodietum subalpinum* Braun-Blanquet 1950 *typicum* sensu Béguin 1974

EPI *Epilobietea angustifolii* Tüxen et Preising ex von Rochow 1951

EPI-04 *Galio-Alliarietalia* Oberdorfer in Görs et T. Müller 1969

EPI-04A *Geo urbani-Alliarion officinalis* Lohmeyer et Oberdorfer in Görs et T. Müller 1969

Cynoglosso germanici-Alliarietum petiolatae Theurillat in Theurillat et Béguin 1985 nom. invers.

typicum

Syn.: *Cynoglossum germanicum*-Gesellschaft Korneck 1974 (Art. 3c)

Alliario petiolatae-Cynoglossetum germanici Géhu, Richard et Tüxen ex Müller in Müller et Oberdorfer 1983 (Art. 3o)

fumarietosum vaillantii Theurillat subass. nov.

Nom. corresp.: *Alliario petiolatae-Cynoglossetum germanici* Géhu, Richard et Tüxen 1972 nom. prov. (Art. 3b)

MUL *Mulgedio-Aconitetea* Hadač et Klika in Klika et Hadač 1944

MUL-04 *Senecioni rupestris-Rumicetalia alpini* Mucina et Karner in Mucina,

Bültmann, Dierssen, Theurillat, Raus et al. 2016

MUL-04A *Rumicion alpini* Rübel ex Scharfetter 1938

Rumici alpini-Aconitetum napelli Aichinger 1933

Appendix: phytosociological nomenclature

Validations of new syntaxa names, lectotypifications and nomenclatural remarks are listed in alphabetical order and in ascending rank, from subassociation to class.

Subassociations

Cynoglosso germanici-Alliarietum petiolatae Theurillat in Theurillat et Béguin 1985 nom. invers.

fumarietosum vaillantii Theurillat et Béguin subass. nov.

Original diagnosis: relevés 1–4, tableau 7, Géhu et al. (1972), relevé 12, tableau 2, Béguin (1974)

Holotypus: relevé 2, tableau 7, Géhu et al. (1972).

Associations

Chenopodio boni-henrici-Arabisetum alpinae (Béguin 1974) ass. nov. et stat. nov. (Holotypus: relevé 7, tableau 2, Béguin, 1974).

(Corresponding name: *Chenopodietum subalpinum arabidetosum alpinae* Béguin 1974 = *Cynoglossogermanici-Alliarietum petiolatae arabidetosum alpinae* Theurillat et Béguin 1985).

Lappulo squarrosae-Asperuginetum procumbentis Braun-Blanquet ex Theurillat et Béguin ass. nov., holotypus relevé 6, table on page 320, Braun-Blanquet & Sutter (1983).

The name of this association (sub ‘*Lappula-Asperugo*-Assoziation’, ‘*Lappuleto-Asperugetum*’, ‘*Lappulo-Asperugetum*’) was proposed for the rock shelters (‘Balmen’) in Graubünden by Braun-Blanquet (1919: 166) and subsequently on several occasions (Braun-Blanquet 1921: 16, 1923: 90, 1949: 139, 1976: 13, Braun-Blanquet & Coaz 1928: 44, Braun-Blanquet et al. 1930: 91, 1931: 128, Lüdi 1921: 296, Rübel 1930: 268) without ever being validly published for lack of a sufficient original diagnosis (Art. 2b). The publication of the relevés (Braun-Blanquet & Sutter 1983: 319) is also not sufficient according to the ICPN, as a type is required on or after 1 January 1979 (Art. 3o). Furthermore, the name-giving species of the genus *Lappula* is missing, as both *L. deflexa* (Wahlenberg) Garcke 1863 and *L. echinata* Gilib 1782 (= *L. squarrosa* (Retz.) Dumort. 1827) occur in the relevés (Art. 3g).

Sisymbrio-Asperuginetum Rebholz ex Oberdorfer 1957. Rebholz (1931 p. 227) described in the Swabian Jura a particular ‘variant (subassociation)’ of Braun-Blanquet’s ‘*Asperugo procumbens-Lappula myosotis*-Assoziation’ in the Alps, dominated by the characteristic species *Asperugo procumbens* and *Sisymbrium austriacum* (‘*Sisymbrium austriacum-reiche-Lappula-Asperugo*-Assoziation’, table on p. 228), but in which *Lappula myosotis* Moench 1794 (= *Hackelia deflexa* (Wahlenberg) Opiz 1839) was missing from the relevés, which invalidated the name *Asperugo procumbentis-Lappuletum myosotis* Braun-Blanquet ex Rebholz 1931 (Art. f), as well as the illegitimate name (Art. 34c) ‘*Sisymbrium austriacum-reiche-Lappula-Asperugo*-Assoziation’. Oberdorfer (1957: 49) refers to this plant community as ‘*Sisymbrio-Asperuginetum* Rebholz 31’ [recte: *Sisymbrio austriaci-Asperuginetum procumbentis* Rebholz ex Oberdorfer 1957], accompanied by a synoptic relevé of Rebholz’s relevés, as a vicariant association of the ‘*Lappulo-Asperuginetum*’ of the Alps. We designate as the lectotype of the name (lectotypus hoc loco) the relevé IV of the table in Rebholz (1931: 228).

Urtico dioicae-Chenopodietum boni-henrici (Braun-Blanquet 1950) Rivas-Martínez et Géhu 1978. This is the replacement name published by Rivas-Martínez & Géhu (1978, p. 380) for the illegitimate name ‘*Chenopodietum subalpinum* Braun-Blanquet 1950’ (Art. 34).

Alliances

Arction alpestre Braun-Blanquet 1976. This alliance, whose name is illegitimate (Art. 34a), was published by Braun-Blanquet (1976: 13) to include the nitrophilous ruderal vegetation dominated by species of the genera *Arctium*, *Artemisia*, *Carduus*, *Cirsium* and *Urtica* in the inner valleys of the Alps, parallel to the *Arction lappae* Tüxen 1937. Two associations formed the original diagnosis, the new association ‘*Galeopsi-Arctietum tomentosae*’ [recte: ‘*Galeopsio tetrahit-Arctietum tomentosae* Braun-Blanquet 1976] from roadsides and a ‘*Polygono-Chenopodietum rubri* Lohmeyer 1950’ from dung heap margins. Syntaxonically, Braun-Blanquet also included the rock shelter association ‘*Lappulo-Asperugetum*’ in the *Arction alpestre*. The alliance thus forms a heterogeneous whole. On page 20, however, Braun-Blanquet assigns his *Polygono brittingeri-Chenopodietum rubri* to the order *Bidentetalia*. Although the *Arction alpestre* Braun-Blanquet 1976 is an illegitimate name, we designate the association ‘*Galeopsio tetrahit-Arctietum tomentosae*’ (Braun-Blanquet 1976: 13) as the lectotype (lectotypus hoc loco) of the name, which is thus a heterotypic synonym of the *Arction lappae* Tüxen 1937, although not mentioned in the EuroVegChecklist.

Chenopodion subalpinum Braun-Blanquet 1948. The illegitimate name of this alliance (Art. 34) is published validly for the Pyrenees in Braun-Blanquet (1948a: 140), with the unique association *Chenopodio-Taraxacetum pyrenaici* Braun-Blanquet 1948. In the text, the alliance is placed in the order

‘*Chenopodietalia*’ and the class ‘*Rudero-Secalieta*’. In reality, this order does not exist in the table of contents, where a footnote (p. 11) mentions that the *Chenopodion subalpinum* belongs to the order ‘*Onopordetalia*’, recently separated from the *Chenopodietalia*, but as the text had already been printed, it was not possible to change it in this sense. At the same time, the alliance is also mentioned as a new alliance in the Alps (Braun-Blanquet, 1948b, 1949), but without sufficient bibliographical reference to the publication on the Pyrenees. The *Chenopodion subalpinum* Braun-Blanquet of the Pyrenees is therefore heterotypic to the *Chenopodion subalpinum* Braun-Blanquet of the Alps. Although the alliance was described in 1949, the bibliographical references for the diagnosis of the name were published in Braun-Blanquet (1950), hence *Chenopodion subalpinum* Braun-Blanquet 1950. In Mucina et al. (2016), the ‘*Chenopodion subalpinum* Braun-Blanquet 1948’ is a synonym of *Rumicion alpini* Scharfetter 1938. However, according to its original diagnosis, this alliance corresponds to the *Arction lappae* Tüxen 1937 (see e.g. Rivas-Martínez et al. 2011).

Onopordion acanthii Braun-Blanquet 1936 ex Braun-Blanquet, Gajewski, Wraber et Walas 1936. The name of this alliance was first invalidly proposed by Braun-Blanquet (1926: 38), as there was no indication of a valid association in its original diagnosis (Art. 2b). It was then incidentally validly published in Braun-Blanquet et al. (1936: 27) with the association ‘*Onopordetum acanthii* Braun-Blanquet ex Braun-Blanquet, Gajewski, Wraber et Walas 1936’, validly published with a synoptic relevé from the Pyrenees. However, this association name is a later heterotypic homonym of the *Onopordetum acanthii* Libbert 1932, described using a relevé from northern Germany (Libbert 1932: 39). It is therefore proposed to conserve the *Onopordetum acanthii* Braun-Blanquet ex Braun-Blanquet, Gajewski, Wraber et Walas 1936, the type of the alliance, instead of the *Onopordetum acanthii* Libbert 1932, which this author places in the ‘*Hordeo-Onopordion*’ alliance with the *Hordeum murinum*-Assoziation. Since Dengler (2002) has typified the name *Hordeo-Onopordion* Libbert 1932 with the association *Hordeetum murini* Libbert 1932, this alliance name becomes a syntaxonomic synonym of *Sisymbrium officinalis* Tüxen, Lohmeyer and Preising ex von Rochow 1951. However, the alliance *Hordeo-Onopordion* Libbert 1932 is the holotype of the name *Chenopodio-Urticetalia* Libbert 1932, which is an earlier, validly published synonym of the name *Sisymbrietalia sophiae* J. Tüxen ex Görs 1966. It is therefore also proposed to conserve the latter name.

Orders

Arctio lappae-Artemisietalia vulgaris Dengler 2002. The name ‘*Artemisietalia vulgaris*’ was validly published by Tüxen (1947) according to Dengler (2002). Its holotype is the alliance ‘*Calystegion sepium*’, also validly published with the association ‘*Petasito hybridi-Aegopodietum*’. According to Dengler too, the second alliance ‘*Arction lappae*’ mentioned in the order *Artemisietalia vulgaris* is invalid in Tüxen (1947). Consequently, the name *Artemisietalia vulgaris* Tüxen 1947 would be an earlier syntaxonomic synonym having priority over the name ‘*Petasito-Chaerophylletalia Moriariu* 1967’ for perennial nitrophilous plant communities in cool locations (*Convolvuletalia sepium* Tüxen ex Moor 1958 following Mucina et al. 2016). Consequently, the name *Artemisietalia vulgaris* Tüxen 1947 should be rejected, as its use would be a permanent source of ambiguity (Art. 36) due to its type, the alliance ‘*Calystegion sepium*’ corresponding to riparian nitrophilous plant communities. According to Dengler (2002: 66), at that point there was no other available name for the order of nitrophilous perennial plant communities in cool locations. Therefore, he published the new name ‘*Arctio lappae-Artemisietalia vulgaris*’ with the alliance ‘*Arction lappae* Tüxen 1937’ as the type. However, the name ‘*Artemisietalia vulgaris*’ was validly published by Tüxen (1947), but with the alliance *Arction lappae* Tüxen 1937 as its holotype (see under *Artemisietalia vulgaris*). The name *Arctio lappae-Artemisietalia vulgaris* Dengler 2002 is therefore superfluous (Art. 29c).

Artemisietalia vulgaris Tüxen 1947. Tüxen (1947: 276) proposed the name of this order, in which he included two alliances, the ‘*Calystegion sepium*’ [recte: *Calystegion sepium*], so named for linguistic reasons rather than *Convolvulion sepium* (p. 287), and the ‘*Arction lappae*’. The *Calystegion sepium* comprises two associations, ‘*Convolvulus sepium-Cuscuta europaea*-Ass.’ and ‘*Petasites hybridus-Aegopodium podagraria*-Ass.’. The first of these two associations is invalid because *Cuscuta europaea* does not appear in the relevés corresponding to this association on p. 153, under the name ‘*Convolvulus*

sepium-Ges.’ (Art. 3f). The second association, *Petasito hybridi-Aegopodietum podagrariae*, is validly published on p. 128 with two relevés. However, *Convolvulus sepium* does not appear in the two relevés given by Tüxen. On p. 129, the alliance ‘*Convolvulion sepii*-Verband’ is referred to an ineffectively published work (Art. 1) by Tüxen (‘Stromtal-Gesellschaften des mittleren Weser-Tales und ihre Stellung in Mittel-Europa mit Beiträgen von W. Pirk (Pilze) und W. Lohmeyer (*Bidentation*). Manuskript’). As a result, the name *Calystegion sepium* was not validly published (Art. 3f), contrary to what Dengler (2002: 66) and Dengler et al. (2003) claim, following a misinterpretation of Article 3f. The second alliance *Arction lappae* contains only the association ‘*Echium vulgare-Melilotus albus*-Ass.’ described on p. 170. Its diagnosis contains two relevés in which *Echium vulgare* L. 1753 is missing, as well as a reference to a particular subassociation with *Artemisia vulgaris* published ineffectively in Tüxen (1942) (Art. 1). Consequently, the association with *Echium vulgare* and *Melilotus albus* on pages 170–175 is invalid. However, on page 119, Tüxen (1947) explicitly stated that ‘The plant names correspond to those used in the ‘Pflanzengesellschaften Nordwestdeutschlands’ (Tx. 1937, 2nd ed. in preparation).’ (‘Die Pflanzen-Namen stimmen also mit denen in den ‘Pflanzengesellschaften Nordwestdeutschlands’ (Tx. 1937, 2. Aufl. in Vorbereitung) gebrauchten überein.’), which can be extended incidentally to the plant community names too. This is further supported by the numerous references to Tüxen (1937) for plant community names throughout Tüxen (1947) (e.g. pp. 170, 176) and by the unambiguous reference to Tüxen (1937) on p. 286, where the name *Arction lappae* was validly published on p. 21 and contains *Artemisia vulgaris* in its original diagnosis. The name *Artemisietalia vulgaris* was therefore validly published in Tüxen (1947) and the alliance *Arction lappae* Tüxen 1937 is its holotype.

Passarge (1993 p. 368) chose the association *Chenopodio boni-henrici-Urticetum urentis* Tüxen 1937 [recte: *Urtico urentis-Chenopodietum boni-henrici* nom. invers.] as the lectotype for the *Arction lappae* Tüxen 1937. The name *Chenopodio boni-henrici-Urticetum urentis* Tüxen 1937 was neotypified by Dengler (2002 p. 67).

Hackelio deflexae-Blitetalia virgati Mucina et Theurillat ord. nov. Mucina (in Mucina et al. 2016: 193) published the new order ‘*Hackelio deflexae-Blitetalia foliosi*’ to include an alliance of rock shelters in the mountains of central Europe, the *Erysimo wittmannii-Hackelion deflexae*, published by Bernátová (1986: 55) with an association from Slovakia (*Hackelio deflexae-Chenopodietum foliosi* Bernátová 1986). However, the name of the order is invalid (Art. 3l) because ‘*Blitum foliosum*’ does not exist as a validly published species name (Euro+Med 2025+ (Euro+Med PlantBase, <https://euoplusmed.org/>), IPNI (International Plant Name Index, <https://www.ipni.org/>), WFO (World Flora Online, <https://www.worldfloraonline.org/>)). We therefore validate here the order name *Hackelio deflexae-Blitetalia virgati* Mucina et Theurillat ord. nov. with the alliance *Erysimo wittmannii-Hackelion deflexae* Bernátová 1986 as holotypus. The diagnostic species of the order are identical to those mentioned for the alliance (Bernátová, 1986: 55).

Onopordetalia acanthii Braun-Blanquet et Tüxen ex Klika in Klika et Hadač 1944. The name ‘*Onopordetalia*’ was proposed by Braun-Blanquet & Tüxen (1943: 6) with an insufficient diagnosis (Art. 2b). The name ‘*Onopordetalia* Braun-Blanquet & Tüxen 1944’ [recte: 1943] was incidentally validly published in Klika & Hadač (1944: 201) with the two alliances ‘*Onopordion* Braun-Blanquet 1926’ and ‘*Arction lappae* Tüxen 1937’. Thanks to the reference to Klika & Novák (1941) on pages 249 and 257 regarding bibliographic citations (see Chytrý et al. 2015: 278–279), the two alliances each have a sufficient diagnosis, with the *Onopordion* being validated incidentally (*Onopordion* Braun-Blanquet ex Klika in Klika & Novák 1941). This alliance is then automatically the type of the order (Art. 19), but it is a heterotypic posterior homonym of the *Onopordion acanthii* Braun-Blanquet ex Braun-Blanquet, Gajewski, Wraber et Walas 1936 (see under *Onopordion*), which must be conserved.

Senecioni rupestris-Rumicetalia alpini Mucina et Karner in Mucina, Bültmann, Dierssen, Theurillat, Raus et al. 2016. Karner & Mucina (1993) created the new order *Rumicetalia alpini* with the alliance ‘*Rumicion alpini* Rübel ex Klika in Klika et Hadač 1944 as the type, whose name is invalid (Art. 2b). Mucina and Karner (in Mucina et al. 2016: 77) then published the new name ‘*Senecio rupestris-Rumicetalia alpini*’ with the alliance *Rumicion alpini* Rübel ex Scharfetter 1938 as the type.

In Scharfetter (1938: 261), the diagnose of the alliance name contains two elements, the ‘*Urticetum*’, which is a nomen nudum and the ‘*Rumicetum alpini*’, which is a superfluous name (Art. 29c) as it contains in synonymy the association ‘*Rumex alpinus-Aconitum napellus*-Assoziation’ validly published by Aichinger (1933: 158). We typify here the *Rumici alpini-Aconitetum napelli* Aichinger 1933 with relevé 1 (lectotypus hoc loco) in Table 38 (Aichinger 1933: 160).

Classes

Artemisietea vulgaris Lohmeyer, Preising et Tüxen ex Pignatti 1952. The name *Artemisietea vulgaris* was first published by Tüxen (1950: 155), but invalidly (*Artemisietea vulgaris* Lohmeyer, Preising and Tüxen 1950; Art. 2b), for nitrophilous hems of seashores, riparian zones, edges, hedgerows and ruderal plant communities in the Eurosiberian region. The validity of the name was then attributed to Rochow (1951) (e.g. Theurillat et al. 1995, Mucina et al. 2016), which is incorrect due to the lack of a sufficient original diagnosis in Rochow, where the class *Artemisietea vulgaris* only included the order ‘*Onopordetalia* Braun-Blanquet et Tüxen 1943’, a name that is invalid in both Tüxen & Braun-Blanquet (1943: 6) and Rochow (1951) (Art. 2b). In Rochow, the *Onopordetalia* included the two alliances ‘*Onopordion* Braun-Blanquet 1926’ and ‘*Eu-Arction lappae* Tüxen 1937 em. Sissingh 1946’. For the first alliance, the name is invalid in Braun-Blanquet (1926: 38) (Art. 2b) (see above). In Rochow, the alliance contains the ‘*Echio-Melilotus*-ass. Tüxen 1942’. The name of this association is validly published by Rochow, but the two relevés of its diagnosis do not contain any species of the genus *Onopordum* and the name ‘*Onopordion* Braun-Blanquet ex Rochow 1951’ is therefore invalid (Art. 3f). For the *Arction lappae*, there is a sufficient bibliographic reference to Tüxen (1937) where the name is validly published with four associations. However, none of the original diagnoses of these associations includes a species of the genus *Onopordum*. It follows that the name ‘*Onopordetalia* Braun-Blanquet et Tüxen ex von Rochow 1951’ is invalid (Art. 3f) and therefore that the name ‘*Artemisietea vulgaris* Lohmeyer, Preising et Tüxen ex Rochow 1951’ is also invalid for lack of a sufficient diagnosis (Art. 2b).

To our knowledge, the name of the class was first validly published by Pignatti (1952: 306). The diagnosis of the class included the order ‘*Onopordetalia* Braun-Blanquet et Tüxen 1943’ with the two alliances ‘*Onopordion* Braun-Blanquet 1926’ and ‘*Eu-Arction lappae* Tüxen 1937 em. Sissingh 1945’. For the *Onopordion* there was no bibliographical reference to Braun-Blanquet (1926) (where the name is invalid, see above). However, the alliance included the association ‘Ass. ad *Erigeron canadense* et *Broussonetia papyrifera* Pignatti 1953’ [recte: 1952] with a synoptic relevé containing *Onopordon acanthium* L. 1753. The name ‘*Onopordion acanthii* Braun-Blanquet ex Pignatti 1952’ was then incidentally validly published, as is the name of the order ‘*Onopordetalia acanthii* Braun-Blanquet ex Pignatti 1952’. Similarly, the name of the class ‘*Artemisietea vulgaris* Lohmeyer, Preising et Tüxen ex Pignatti 1952’ was also incidentally validly published because the synoptic relevé of the association with *Erigeron canadense* and *Broussonetia papyrifera* also included *Artemisia vulgaris* L. 1753, in addition to the fact that there is a sufficient bibliographical reference to Tüxen (1937) for the ‘*Eu-Arction*’ alliance, whose original diagnosis includes associations with *A. vulgaris*.

According to Dengler et al. (2003), the nitrophilous communities of ‘*Artemisietea vulgaris* Lohmeyer, Preising et Tüxen ex Rochow 1951’, ‘*Epilobietea angustifolii* Tüxen et Preising ex von Rochow 1951’, ‘*Galio-Urticetea* Passarge ex Kopecký 1969 and *Agropyretea intermedio-repentis* Oberdorfer, Th. Müller et Görs ex Th. Müller et Görs 1969 form a single class. As the name ‘*Artemisietea vulgaris* Lohmeyer, Preising et Tüxen ex Rochow 1951’ retained for this grouping is invalid, the earliest available name is ‘*Epilobietea angustifolii* Tüxen et Preising ex von Rochow 1951’, which must be used if this syntaxonomic concept is to be retained (Art. 25).

Erweiterte deutsche Zusammenfassung

Einleitung – Höhlen am Fuß von Kalksteinfelsen oder Felsüberhänge (auch ‘Balmen’ genannt) haben schon immer natürlichen Schutz geboten. Die kleinen, zwischen 2 und 5 m tiefen Höhlen unterschiedlicher Größe und Form (Abb. 2a und b, Anhang E4) dienen außerhalb der Saison hauptsächlich als Ruheplätze und Unterschlupf für Wildtiere, insbesondere Gämsen (*Rupicapra rupicapra* L.) (Rübel 1930). Diese vor Niederschlägen geschützten Orte können seltene und spezialisierte Arten beherbergen (Bernátová 1987), die als Relikte vom Ende der letzten Eiszeit oder vom Beginn des Holozäns gelten. Sie bilden einzigartige nitrophile Pflanzengesellschaften (Braun-Blanquet & Sutter 1983, Mucina et al. 2016, Bernátová et al. 2024). Aufgrund ihrer Seltenheit wurden die Felsüberhänge am Fuß der Jurafelsen nicht beschrieben. Die Ziele dieser Arbeit sind (1) die Beschreibung der spezialisierten Vegetation, die mit Felsüberhängen im Jura verbunden ist, wobei die Klassifizierung zuvor beschriebener Pflanzengemeinschaften überdacht wird, (2) die Einordnung dieser Vegetation in ihren landschaftlichen Kontext mithilfe einer vereinfachten synsoziologischen Methode und (3) die Kommentierung und gesonderte Validierung der Namen verwandter nitrophiler Syntaxa, die Teil der EuroVegChecklist sind (Mucina et al. 2016), aus nomenklatorischer Sicht.

Material & Methoden – Der Jura ist ein 350 km langes, im Allgemeinen nach Nordosten verlaufendes Kalksteinmassiv, das sich an der Grande Chartreuse nördlich von Grenoble (Isère, Frankreich) von den Alpen trennt. Er kulminiert in der ersten Antiklinale nordwestlich von Genf (Ain, Frankreich) am Crêt de la Neige (1720 m) (Anhang E1). Geologisch entsprechen die subvertikalen Klippen widerstandsfähigen Schichten des Portlandiums und des Kimmeridgiums, die auf weniger widerstandsfähigen Schichten aus Mergelkalksteinen des Sequaniums und des Aargaus ruhen. Zur Basis des Kimmeridgiums hin befindet sich eine mäßig widerstandsfähige ‘Übergangsformation’, die schneller erodiert und die Bildung von Felsüberhängen durch periglaziale Erosion ermöglicht (Abb. 2–3 Anhang E4). Geomorphologisch hat die Karst- und Periglazialerosion kleine Kataklinaltäler, sogenannte ‘Ruz’, geschaffen, die in die Flanke einer Antiklinale im südwestlichen Jura eingeschnitten sind (Anhang E2). Aubert (1965) unterteilte den Jura in den ‘Felsjura’, der sich von Pontarlier bis zu den Tälern des Ain und Valserine erstreckt und während der letzten Vereisung (Würm) vom Jura-Inlandeis bedeckt wurde, wodurch der zuvor entstandene Boden geformt wurde, und den ‘Grasjura’, der während der letzten Vereisung nicht vom Eis bedeckt wurde und in dem vorzeitliche Böden überdauern konnten. Geografisch wird der Jura nach Thurmann (1849) in vier Teile unterteilt: den Süd-, West-, Zentral- und Ostjura (Anhang E1). Bioklimatisch gesehen gibt es im Jura einen echten subalpinen Vegetationsgürtel (Béguin 1974, Theurillat 1991, Vittoz 1998), der auf etwa 1250–1300 m ü. M. in der Region Reculet (westlicher Jura) beginnt.

Die Vegetation der Felsüberhänge wurde mit pflanzensoziologischen Aufnahmen (Braun-Blanquet 1964) untersucht, die von Béguin (Tab. 2, 1974) aus Le Reculet (Westjura) und dem Creux du Van (Zentraljura) durchgeführt wurden. Die Analyse der Vegetationslandschaft (Synsoziologie s.l.) folgt einer vereinfachten Methode nach Béguin (1999), unter Verwendung einer Vegetationskarte im Maßstab 1:5000. Die Taxonomie der Gefäßpflanzen folgt Euro+Med 2006+ (Euro+Med PlantBase, <https://euoplusmed.org/>). Die Nomenklatur der Syntaxa über dem Assoziationsrang folgt Mucina et al. (2016) und Aeschmann et al. (2004); die der Assoziationen folgt Béguin (1974) und Theurillat & Béguin (1985). Die Soziologie der Taxa folgt Aeschmann et al. (2004) und die Lebensformen Landolt et al. (2010). Die Zitation des Internationalen Codes der pflanzensoziologischen Nomenklatur (Artikel) bezieht sich auf Theurillat et al. (2021).

Ergebnisse – Die Subassoziation *Chenopodietum subalpinum arabidetosum alpinae* Béguin 1974 der Felsüberhänge der Region Reculet (Hochjura) wird in den Rang einer Assoziation als *Chenopodio boni-henrici-Arabidetum alpinae* ass. nov. und stat. nov. erhoben (s. Anhang E5). In der Assoziation dominieren nitrophile Arten der *Artemisietea vulgaris* (*Chenopodium bonus-henricus*, *Urtica dioica*), begleitet von Graslandarten (*Galium album*, *Festuca pratensis*, *Dactylis glomerata*) (Tab. 1). Ihr Vorkommen ist einerseits auf eine spezifischen Kombination tektonischer, stratigraphischer, petrographischer, geomorphologischer und klimatischer Faktoren zurückzuführen, die die Bildung von Felsüber-

hängen ermöglichen, und andererseits auf einen nitrophilen Faktor. Der steile Hang auf dem weichen Sequanium-Kalkstein unterhalb des Felsvorsprungs ermöglicht den Abtransport von Material aus der Erosionszone durch die Schwerkraft (Abb. 1 und 2a). Die Stickstoffversorgung an der flachen Basis des Felsvorsprungs erfolgt durch den Kot von Gämsen und seltener von Schafen, Steinböcken und Färsen.

Landschaftlich gesehen gehört das *Chenopodio-Arabidetum* zum Kalkfelsenkomplex, der eine katenalet Einheit der Hypogeosigmassoziationsebene (Theurillat 1992) bildet, nämlich das *Potentillo caulescentis-Hieracieto humilis-Hypogeosigmetum*, bestehend aus (a) Felsspaltenassoziationen, (b) den Grasnarben an den Hängen und Ebenen und (c) der Basis der Felsvorsprünge am Fuße der Klippen (Tab. 2).

Discussion – Im Juragebirge sind Felsüberhänge auf den Westjura beschränkt, da im Zentral- und Ostjura die ‚Übergangsformation‘ an der Basis des Kimmeridgiums (Hartgestein) fehlt (Anhang E3). Auch die Mergel-Kalk-Schicht des Sequaniums ist schwächer, was die Bildung von Ruz und Steilhängen nicht begünstigt. Daher ist auch die Geomorphologie der Klippen unterschiedlich (Antiklinalkämme, Kare oder geschlossene Becken) (Anhang E2). Infolgedessen sind die Felsüberhänge aufgrund der Struktur der Klippen und der Auffüllung mit Schutt oder Moränenablagerungen, die nicht durch die Schwerkraft abtransportiert werden, nahezu unsichtbar (Anhänge E6 und E7). Am Fuße der großen Klippen des Creux du Van im Zentraljura (Anhang E6) entspricht die Vegetation einer neuen Subassoziation *fumarietosum vaillantii* des *Cynoglosso-Alliarietum* (Anhang E8). Es handelt sich um eine Übergangssituation zwischen dem *Chenopodio boni-henrici-Arabidetum alpinae* und dem *Cynoglosso-Alliarietum typicum* aus Rheinland-Pfalz (Deutschland; Korneck, 1974). Im Kaisertal (Tirol, Österreich) schließt sich die Assoziation *Cynoglosso germanici-Chenopodietum boni-henrici* (Smettan 1981, Mucina 1993) dem *Chenopodio-Arabidetum* an. Bei ausgeprägterem und vor Niederschlag geschütztem Felschutz ist die Vegetation der Ruheplätze durch xerophile nitrophile Therophyten (Rübel 1930) der Klasse *Sisymbrietea* gekennzeichnet, wie im Fall des *Lappulo-Asperuginetum procumbentis* aus den Schweizer Alpen (Braun-Blanquet 1919, Braun-Blanquet & Sutter 1983). Dieser ungültig veröffentlichte Name wird als *Lappulo squarrosae-Asperuginetum procumbentis* (Anhang) validiert. Eine vikariierende Assoziation, das *Sisymbrio austriaci-Asperuginetum procumbentis*, wurde in den Felsüberhängen des Donautals der Schwäbischen Alb in Süddeutschland beschrieben (Rebholz 1931, Oberdorfer 1957) (siehe Anhang). Eine weitere vikariierende Assoziation mit *Asperugo procumbens* findet sich in Felsüberhängen am Fuße der Küstenkalkklippen der kleinen Insel Stora Karlsö westlich von Gotland (Schweden) (*Asperugo procumbens*-Gesellschaft, Westhoff et al. 1983). Mehrere Assoziationen von Felsüberhängen wurden auch aus der montanen Stufe der Westkarpaten (Veľká Fatra, Chočské vrchy) in der Slowakei beschrieben (Bernátová 1986, 1991, Bernátová & Obuch 1991, 1995): *Hackelio deflexae-Chenopodietum foliosi* Bernátová 1986, *Arenario serpyllifoliae-Descurainietum sophiae* Bernátová 1991, *Taraxaco laevigati-Sisymbrietum austriaci* Bernátová 1991, *Poo nemoralis-Hackelietum deflexae* Bernátová 1991, *Arabido turritae-Sisymbrietum strictissimi* Bernátová 1991 und *Cortuso matthioli-Papaveretum tatricum* Bernátová 1991 (Anhang E8).

Laut Mucina et al. (2016) gehört die therophytenreiche zoogene Vegetation von Felsüberhängen in den Gebirgen Mitteleuropas zum Verband *Erysimo witmannii-Hackelion deflexae* und zur Ordnung *Hackelio deflexae-Blitetalia virgati* (siehe Anhang 8) innerhalb der Klasse *Sisymbrietea*. Die Individualität des *Erysimo-Hackelion* ist für die sechs oben genannten slowakischen Assoziationen, die eine bemerkenswerte floristische und soziologische Homogenität aufweisen, voll gerechtfertigt. Im Vergleich dazu weisen Felsüberhangs-Assoziationen in anderen Regionen signifikante Unterschiede in der floristischen Zusammensetzung (Anhang E8), aber auch im soziologischen Spektrum und den Lebensformen auf (Beilage S1 und S2). Sie gehören daher zu anderen Verbänden, wie dem *Arction lappae* für das *Chenopodio boni-henrici-Arabidetum alpinae*, dem *Sisymbrio officinalis* für das *Lappulo squarrosae-Asperuginetum procumbentis* und dem *Geo-Alliarion* für das *Cynoglosso germanici-Alliarietum petiolatae fumarietosum vaillantii* (siehe syntaxonomisches Schema).

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Author contribution statement

C.B. conceived the idea of the study and wrote the first draft of the paper. E.D.M. performed the numerical analyses. J.-P.T. contributed to the writing and did the phytosociological and nomenclatural analyses.

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Supplements

Supplement S1. Sociological characterisation, mainly at class level, of the species in the relevés that make up the original diagnoses of the studied rock shelter and resting place plant communities (Supplement E8).

Beilage S1. Soziologische Charakterisierung, vorwiegend auf Klassenebene, der Arten in den Vegetationsaufnahmen der ursprünglichen Diagnosen der untersuchten Felsüberhangs- und Ruheplatzpflanzengesellschaften (Beilage E8).

Supplement S2. Proportion of life forms according to Landolt et al. (2010) within the species of the relevés forming the original diagnosis of the studied rock shelter and resting place plant communities (Supplement E8).

Beilage S2. Anteil der Lebensformen nach Landolt et al. (2010) innerhalb der Arten der Aufnahmen der Erstdiagnose der untersuchten Felsüberhangs- und Ruheplatzpflanzengesellschaften (Supplement E8).

Supplements Additional supporting information may be found in the online version of this article.
Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Location of the study area.
Anhang E1. Lage des Untersuchungsgebietes.

Supplement E2. Semi-schematic block diagram of the Haut-Jura, from the western Jura to the central Jura.
Anhang E2. Halbschematisches Blockdiagramm des Hochjuras, vom westlichen zum zentralen Jura.

Supplement E3. Stratigraphic scale and semi-schematic profile of a cliff in the central Jura.
Anhang E3. Stratigraphischer Maßstab und halbschematisches Profil einer Klippe im Zentraljura.

Supplement E4. Rock shelters and soft tourism in the Reculet region.
Anhang E4. Felsüberhänge und sanfter Tourismus in der Region Reculet.

Supplement E5. Numerical analyses of the evolution of *Chenopodietum subalpinum* in the Reculet region.

Anhang E5. Numerische Analyse der Entwicklung des *Chenopodietum subalpinum* in der Region Reculet.

Supplement E6. Glacial cirque of Creux du Van (central Jura).

Anhang E6. Gletscherkessel des Creux du Van (zentraler Jura).

Supplement E7. Ridge without rock shelter in the Chasseral (central Jura).

Anhang E7. Grat ohne Felsüberhang im Chasseral (zentraler Jura).

Supplement E8. Synoptic table of the relevés of the original descriptions of overhang plant communities and resting places (*Arction lappae*, *Geo-Alliarion*, *Sisymbrium officinalis*, *Erysimo-Hackelion deflexae*).

Anhang E8. Übersichtstabelle der Vegetationsaufnahmen der Originalbeschreibungen von Überhang-Pflanzengesellschaften und Ruheplätzen (*Arction lappae*, *Geo-Alliarion*, *Sisymbrium officinalis*, *Erysimo-Hackelion deflexae*).

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Supplement S1. Sociological characterisation, mainly at class level, of the species in the relevés that make up the original diagnoses of the studied rock shelter and resting place plant communities (Supplement E8). The numbers correspond to the frequency of occurrence (%) in relation to the total number of species in the relevés of the original diagnoses.

Beilage S1. Soziologische Charakterisierung, vorwiegend auf Klassenebene, der Arten in den Vegetationsaufnahmen der ursprünglichen Diagnosen der untersuchten Felsüberhangs- und Ruheplatzpflanzengesellschaften (Anhang E8). Die Zahlen entsprechen der Häufigkeit des Vorkommens (%) im Verhältnis zur Gesamtzahl der Arten in den Aufnahmen der ursprünglichen Diagnosen.

Class	Artemisietea vulgaris						Epilobietea angustifolii		Sisymbrietea																																																																																																																																																																											
	Artemisietalia						Galio-Alliarietalia		Sisymbrietalia sophiae				Hackelio deflexae-Blitetalia virgati																																																																																																																																																																							
	Arction lappae						Geo-Alliarion		Sisymbrian officinalis				Erysimo witmannii-Hackelion deflexae																																																																																																																																																																							
	Chenopodio boni-henrici-Arabidetum alpinae	Cynoglosso officinalis-Chenopodietum boni-henrici	Cirsium eriophorum-Rumex obtusifolius community	Alchemillo-Chenopodietum boni-henrici prov.	Urtico-Chenopodietum boni-henrici sisymbriosum	Urtico-Chenopodietum boni-henrici typicum	Cynoglosso germanici-Alliarietum fumaretosum	Cynoglosso germanici-Alliarietum typicum	Asperugo procumbens-Gesellschaft	Sisymbrio austriacae-Asperuginetum procumbentis	Lappulo squarrosae-Asperuginetum procumbentis	Cirsium arvensis-Hackelia deflexa community	Hackelio deflexae-Chenopodietum foliosi	Arenario serpyllifoliae-Descurainietum sophiae typicum	Taraxaco laevigati-Sisymbrietum austriaci	Poa nemoralis-Hackelietum deflexae	Arabido turriacae-Sisymbrietum strictissimi	Cortuso matthioli-Papaveretum tatrici																																																																																																																																																																		
Syntaxon	6	2	14	3	10	36	5	5	2	9	8	3	7	14	9	13	5	7																																																																																																																																																																		
Number of relevés	rs	rs	rp	rp	rp	rp	rs	rp	rs	rs	rs	rp	rs	rs	rs	rs	rs	rs																																																																																																																																																																		
Habitat (rock shelter = rs, resting place = rp)	16	13	18	10	12	20	11	10	8	10	14	14	19	21	21	20	22	21																																																																																																																																																																		
Number of classes	68	22	103	18	44	106	31	27	12	30	32	30	70	120	97	107	84	66																																																																																																																																																																		
Number of species	Artemisietea vulgaris						Artemisietalia vulgaris		Galio-Alliarietalia				Epilobietea angustifolii						Sisymbrietea officinalis						Stellarietea mediae						Polygono-Poetea annuae						Molinio-Arrhenatheretea						Mulgedio-Aconitetea + Rumicetalia						Festuco-Brometea						Trifolio-Geranietea						Crataego-Prunetea						Betulo carpaticae-Alnetea viridis						Carpino-Fagetea						Quercetea pubescentis						Quercetea robori-sessiliflorae						Piceetea excelsae						Erico-Pinetea						Elyno-Seslerietea						Thlaspietea rotundifolii						Asplenietea trichomanis						Koelerio-Corynephoretea						Juncetea trifidi						Filipendulo-Convulvuletea						Salicetea herbaceae						Pyrolo-Pinetea						Montio-Cardaminetea						Calluno-Ulicetea						Carici rupestris-Kobresietea						Scheuchzerio-Caricetea fuscae						-					
1,5	4,5	1,9	11,1	4,5	3,8	3,2	3,7	8,3	3,3	3,1	3,3	1,7						2,1	1,9	2,4	1,5																																																																																																																																																															
Artemisietalia vulgaris	2,9	13,6	1,9	11,1	9,1	2,8	3,2	3,7	6,7		3,1	2,9								1,7	2,1	2,8	3,6	4,5																																																																																																																																																												
Galio-Alliarietalia	2,9	4,5	5,8	3,8			16,1	25,9	25,0	10,0	3,1		2,9	1,7	2,1	2,8	3,6	4,5																																																																																																																																																																		
Onopordetalia acanthii	4,5		1,9	2,3			0,9	8,3		3,3	12,5	13,3	1,4	3,3	2,1	1,9	2,4	1,5																																																																																																																																																																		
Agropyretalia intermedii-repentis	1,5	4,5	1,0	5,6	4,5	3,8	3,2	16,7		10,0	9,4	1,4		1,7	1,0																																																																																																																																																																					
Epilobietea angustifolii	2,9	4,5	2,9	5,6	2,3	1,9	7,4		13,3				1,4	1,7	2,1	6,5	4,8	4,5																																																																																																																																																																		
Sisymbrietea officinalis	6,8					2,8	3,2	8,3		16,7	15,6	10,0	2,9	2,5	3,1	0,9	2,4	3,0																																																																																																																																																																		
Stellarietea mediae	4,4	1,9		5,6	6,8	10,4	3,2	16,7		33,3	15,6	13,3	2,9	5,8	9,3	1,9	9,5	3,0																																																																																																																																																																		
Polygono-Poetea annuae	1,9		11,1	11,4	3,8	3,1		1,2																																																																																																																																																																												
Molinio-Arrhenatheretea	23,5	13,6	32,0	22,2	31,8	33,0	16,1	7,4	8,3	3,3	9,4	4,3		6,7	5,2	4,7	6,0	6,1																																																																																																																																																																		
Mulgedio-Aconitetea + Rumicetalia	13,2	12,6		11,1	11,4	9,4	6,5	3,7	1,4				1,7	1,9		2,4	1,5																																																																																																																																																																			
Festuco-Brometea	7,4	9,1	8,7	2,3			4,7	6,3		3,3	18,6		16,7	12,4	11,2	11,9	3,0																																																																																																																																																																			
Trifolio-Geranietea	4,4	4,5	2,9	0,9			7,4		6,3		6,7	12,9	12,5	10,3	10,3	10,7	4,5																																																																																																																																																																			
Crataego-Prunetea	9,1		3,2					6,3		6,7	7,1	5,8	5,2	5,6	3,6	1,5																																																																																																																																																																				
Betulo carpaticae-Alnetea viridis	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
Carpino-Fagetea	7,4	13,6	1,9	5,6	1,9		3,7		2,9				1,7	1,0	1,9	2,4																																																																																																																																																																				
Quercetea pubescentis	1,5	3,2					6,3		6,7	7,1		5,8	5,2	5,6	3,6	1,5																																																																																																																																																																				
Quercetea robori-sessiliflorae	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
Piceetea excelsae	1,9		2,3			4,7	7,4		6,3		6,7	7,1		5,8	5,2	5,6	3,6	1,5																																																																																																																																																																		
Betulo carpaticae-Alnetea viridis	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
Carpino-Fagetea	7,4	13,6	1,9	5,6	1,9		3,7		2,9				1,7	1,0	1,9	2,4																																																																																																																																																																				
Quercetea pubescentis	1,5	3,2					6,3		6,7	7,1		5,8	5,2	5,6	3,6	1,5																																																																																																																																																																				
Quercetea robori-sessiliflorae	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
Piceetea excelsae	1,9		2,3			4,7	7,4		6,3		6,7	7,1		5,8	5,2	5,6	3,6	1,5																																																																																																																																																																		
Betulo carpaticae-Alnetea viridis	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
Carpino-Fagetea	7,4	13,6	1,9	5,6	1,9		3,7		2,9				1,7	1,0	1,9	2,4																																																																																																																																																																				
Quercetea pubescentis	1,5	3,2					6,3		6,7	7,1		5,8	5,2	5,6	3,6	1,5																																																																																																																																																																				
Quercetea robori-sessiliflorae	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
Piceetea excelsae	1,9		2,3			4,7	7,4		6,3		6,7	7,1		5,8	5,2	5,6	3,6	1,5																																																																																																																																																																		
Betulo carpaticae-Alnetea viridis	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
Carpino-Fagetea	7,4	13,6	1,9	5,6	1,9		3,7		2,9				1,7	1,0	1,9	2,4																																																																																																																																																																				
Quercetea pubescentis	1,5	3,2					6,3		6,7	7,1		5,8	5,2	5,6	3,6	1,5																																																																																																																																																																				
Quercetea robori-sessiliflorae	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
Piceetea excelsae	1,9		2,3			4,7	7,4		6,3		6,7	7,1		5,8	5,2	5,6	3,6	1,5																																																																																																																																																																		
Betulo carpaticae-Alnetea viridis	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
Carpino-Fagetea	7,4	13,6	1,9	5,6	1,9		3,7		2,9				1,7	1,0	1,9	2,4																																																																																																																																																																				
Quercetea pubescentis	1,5	3,2					6,3		6,7	7,1		5,8	5,2	5,6	3,6	1,5																																																																																																																																																																				
Quercetea robori-sessiliflorae	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
Piceetea excelsae	1,9		2,3			4,7	7,4		6,3		6,7	7,1		5,8	5,2	5,6	3,6	1,5																																																																																																																																																																		
Betulo carpaticae-Alnetea viridis	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
Carpino-Fagetea	7,4	13,6	1,9	5,6	1,9		3,7		2,9				1,7	1,0	1,9	2,4																																																																																																																																																																				
Quercetea pubescentis	1,5	3,2					6,3		6,7	7,1		5,8	5,2	5,6	3,6	1,5																																																																																																																																																																				
Quercetea robori-sessiliflorae	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
Piceetea excelsae	1,9		2,3			4,7	7,4		6,3		6,7	7,1		5,8	5,2	5,6	3,6	1,5																																																																																																																																																																		
Betulo carpaticae-Alnetea viridis	1,0			25,8			33,3	8,3	10,0	13,3		12,9		5,0	12,4	16,8	14,3	18,2																																																																																																																																																																		
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Supplement S2. Proportion of life forms according to Landolt et al. (2010) within the species of the relevés forming the original diagnosis of the studied rock shelter and resting place plant communities (Supplement E8). The numbers correspond to the frequency of occurrence (%) in relation to the total number of species in the relevés of the original diagnoses. c: herbaceous chamaephyte, d: nanophanerophyte-hemicryptophyte, f: chamaephyte-hemicryptophyte, g: geophyte, h: hemicryptophyte (long-lived), k: hemicryptophyte (short-lived), n: nanophanerophyte, p: phanerophyte, t: therophyte, z: woody chamaephyte. c-h, c-p, g-h, h-t, h-k, k-t, n-p: the plant can occur in one of two given forms, depending on the conditions. For example, c-h means that the plant can be either an herbaceous chamaephyte or a hemicryptophyte.

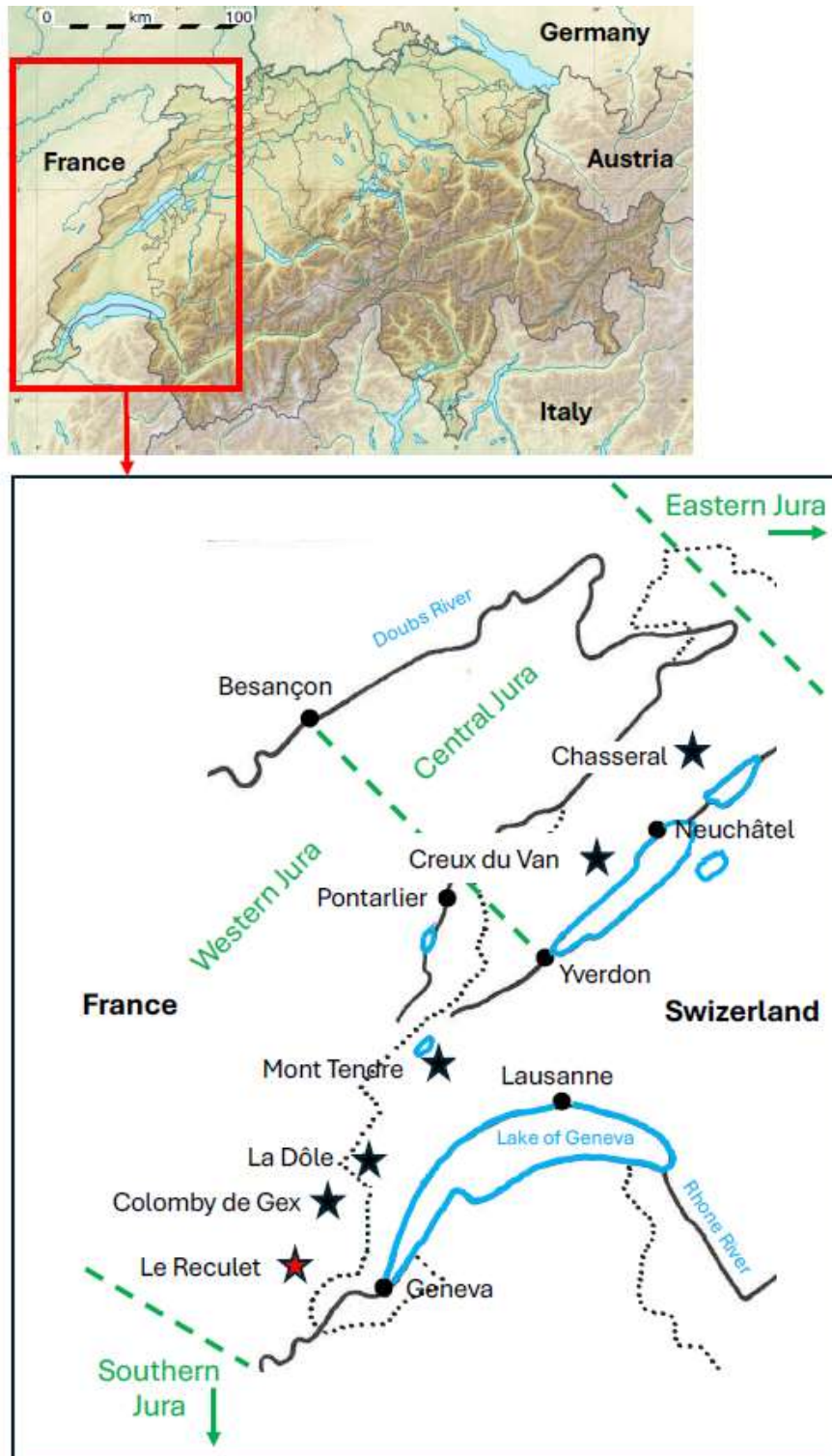
Beilage S2. Anteil der Lebensformen nach Landolt et al. (2010) innerhalb der Arten der Aufnahmen der Erstdiagnose der untersuchten Felsüberhangs- und Ruheplatzpflanzengesellschaften (Anhang E8). Die Zahlen entsprechen der Häufigkeit des Vorkommens (%) im Verhältnis zur Gesamtzahl der Arten in den Aufnahmen der Erstdiagnosen. c: krautiger Chamaephyt, d: Nanophanerophyt-Hemikryptophyt, f: Chamaephyt-Hemikryptophyt, g: Geophyt, h: Hemikryptophyt (langlebig), k: Hemikryptophyt (kurzlebig), n: Nanophanerophyt, p: Phanerophyt, t: Therophyt, z: holziger Chamaephyt. c-h, c-p, g-h, h-t, h-k, k-t, n-p: Die Pflanze kann je nach Bedingungen in einer von zwei angegebenen Lebensformen vorkommen. So bedeutet c-h, dass die Pflanze entweder ein krautiger Chamaephyt oder ein Hemikryptophyt sein kann.

[illegible]

Béguin et al.: The nitrophilous vegetation of rock shelters on limestone in the Haut-Jura (Ain, France) in a European context. – *Tuexenia* 45 (2025).

Supplement E1. Location of the study area.

Anhang E1. Lage des Untersuchungsgebietes.

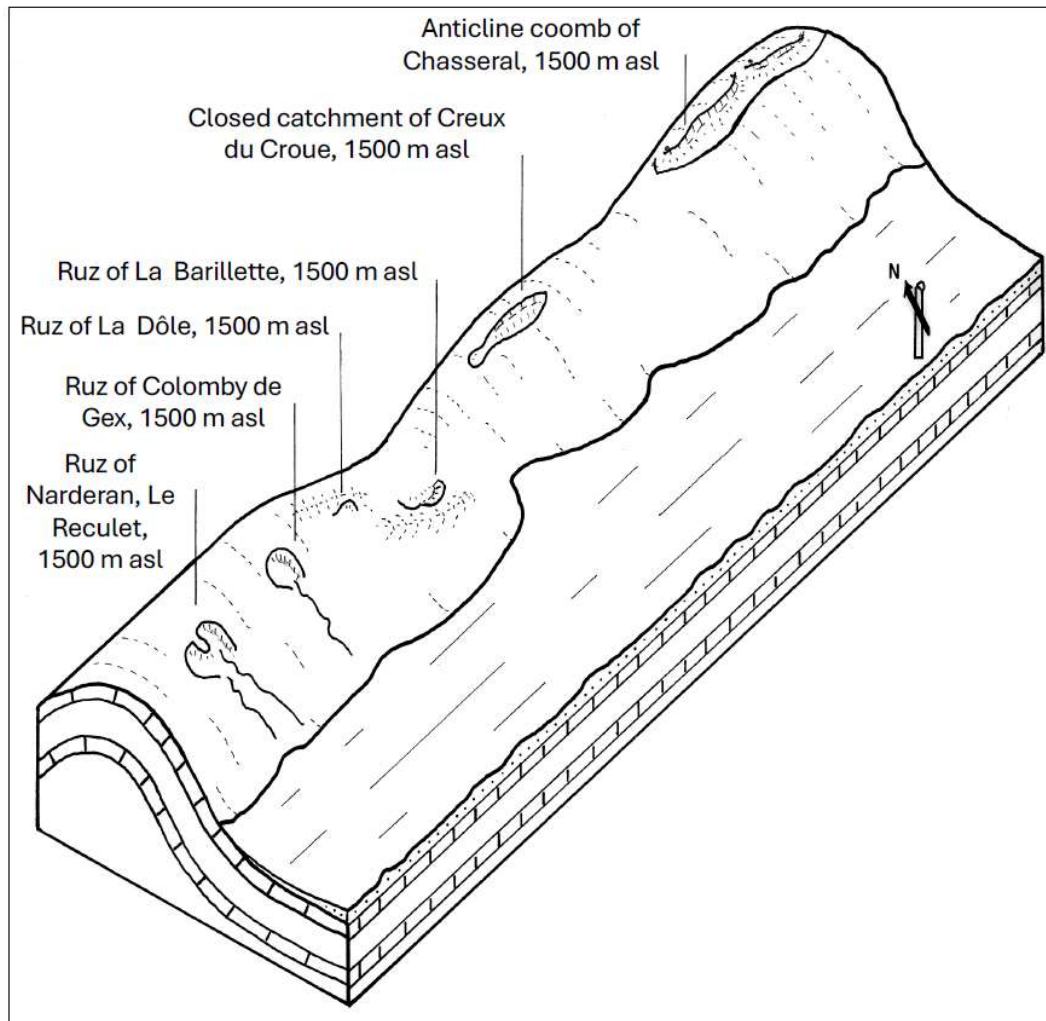


Above is a relief map of Switzerland (https://commons.wikimedia.org/wiki/File:Switzerland_relief_location_map.jpg). The red inset shows the location of the study area (marked with a red star) within the Jura mountain range. Geographical subdivisions of the Jura range (green) after Thurmann (1849).

Béguin et al.: The nitrophilous vegetation of rock shelters on limestone in the Haut-Jura (Ain, France) in a European context. – *Tuexenia* 45 (2025).

Supplement E2. Schematic block diagram of the Haut-Jura, from the western Jura to the central Jura.

Anhang E2. Halbschematisches Blockdiagramm des Hochjuras, vom westlichen zum zentralen Jura.

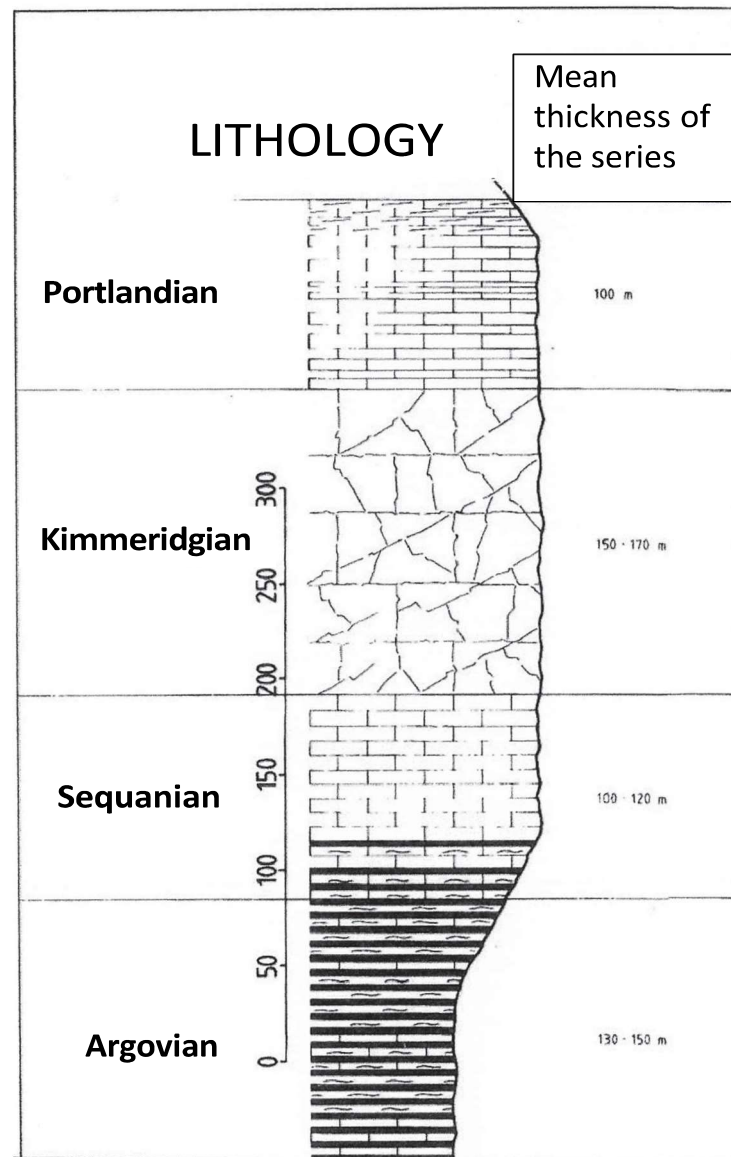


The semi-schematic block diagram of the Haut-Jura shows the presence of deep cataclinal ruz cut into a thick layer of marl limestone in the western Jura, which are typical of the Haute Chaîne (see Fig. 1). These ruz contrast with the anticlinal combes of the central Jura, which have no "transitional formation" (F5a and F5b in Fig. 3) at the base of the hard, high-strength Kimmeridgian rocks, as one can see in Supplement E3. As a result, the central Jura does not provide a geomorphological setting conducive to the formation of rock shelters, as illustrated in Supplement E7. [The figure is not to scale].

Béguin et al.: The nitrophilous vegetation of rock shelters on limestone in the Haut-Jura (Ain, France) in a European context. – *Tuexenia* 45 (2025).

Supplement E3. Stratigraphic scale and semi-schematic profile of a cliff in the central Jura (Vue des Alpes, central Jura, canton of Neuchâtel, after Méia 1992).

Anhang E3. Stratigraphischer Maßstab und halbschematisches Profil einer Klippe im Zentraljura (Vue des Alpes, zentraler Jura, Kanton Neuchâtel, nach Méia 1992).



There is no "transitional formation" at the base of the Kimmeridgian. This means that the formation of rock shelters with a structural flat on the Kimmeridgian, on which the *Chenopodio-Arabidetum alpinae* could develop, cannot be formed.

Méia, J. (1992): Géologie des tunnels de la Béroche et de la Vue des Alpes (Geology of the Béroche and Vue des Alpes galleries) [In French]. – *Mitteilungen der Schweizerischen Gesellschaft für Boden- und Felsmechanik* 126.

Béguin et al.: The nitrophilous vegetation of rock shelters on limestone in the Haut-Jura (Ain, France) in a European context. – *Tuexenia* 45 (2025).

Supplement E4. Rock shelters and soft tourism in the Reculet region.

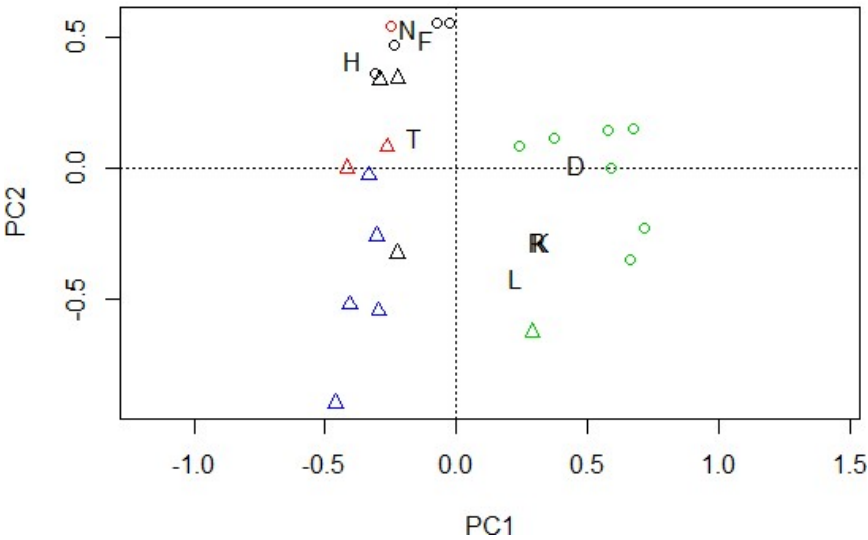
Anhang E4. Felsüberhänge und sanfter Tourismus in der Region Reculet.



Effect of trampling by soft tourism at the foot of a rock shelter: presence of *Capsella bursa pastoris*, *Poa supina*, *Trifolium repens*, *Medicago lupulina*. At the bottom of the ruz, the Nardaran pasture chalet, above which the steep slope of marly limestone evacuates the materials from the altered "Voûtes". (Photo L. Béguin, 16.7.2024)

Supplement E5. Numerical analyses of the evolution of *Chenopodietum subalpinum* in the Reculet region (after Di Maio 2016).

Anhang E5. Numerische Analyse der Entwicklung des *Chenopodietum subalpinum* in der Region Reculet (nach Di Maio 2016).



Triangles: relevés of the *Chenopodietum subalpinum* [= *CS*] *typicum* and *arabidetosum alpinæ* (Béguin 1974; tab. 2); circles: new relevés (2012-2015; Di Maio 2016). The four groups (colours) result from a classification (Euclidian distance, Ward method); black: 4 relevés *CS typicum* and 3 new relevés; red: 1 relevé *CS typicum* and 2 recent relevés; green: relevés 6-12 *CS arabidetosum* and 1 new relevé; blue: 5 new relevés. Indicator values according to Landolt et al. (2010). The first and second axes represent 9.2% and 8.3% of the total variance, respectively. PC1 is positively correlated with the pH indicator value and negatively with the humus value while PC2 is positively correlated with the humidity, nutrients and humus values, and negatively with the light value (see table below). There is therefore a gradient of soil aeration, pH and light on the one hand, and humus content, nutrients and light on the other, along axis 1. This shows a clear difference between the relevés of the *arabidetosum alpinæ* subassociation in the rock shelters (green circles), which are all located in the positive part of axis 1, and the old and new relevés of resting places near the pasture chalets, which are all grouped in the negative part of axis 1 (*Cirsium eriophorum*-*Rumex obtusifolius* community, see Supplement S1).

Indicator value (Landolt et al. 2010)	Axis PC1	Axis PC2
Temperature (T)	-0.225ns	0.168ns
Light (L)	0.325ns	-0.600**
Soil humidity (F)	-0.168ns	0.701***
pH (R)	0.448*	-0.401ns
Nutrients (N)	-0.265ns	0.769***
Humus (H)	-0.560**	0.598**

Pearson correlation values of the mean indicator values for PC1 and PC2 axes. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.



Resting place of the *Chenopodietum subalpinum* at Thoiry-Derrière in the Reculet region (*Cirsium eriophorum*-*Rumex obtusifolius* community, see Supplement E8). (Photo E. Di Maio, 2015)

Béguin et al.: The nitrophilous vegetation of rock shelters on limestone in the Haut-Jura (Ain, France) in a European context. – *Tuexenia* 45 (2025).

Supplement E6. Glacial cirque of Creux du Van (central Jura).

Anhang E6. Gletscherkessel des Creux du Van (zentraler Jura).



Cirque of Creux du Van, carved out of the Soliat anticline (canton of Neuchâtel, Switzerland). A landscape of cliffs with rock ledges, but no rock shelters as such. These may have existed after the retreat of the Würm glacier. Today, they are almost completely filled in by landslides and, locally, by morainal material, and are home to the *Cynoglossa germanici-Alliarietum petiolatae fumarietosum vaillantii* (Supplement E8). (Photo Luc Béguin, 8.9.2023).

Béguin et al.: The nitrophilous vegetation of rock shelters on limestone in the Haut-Jura (Ain, France) in a European context. – *Tuexenia* 45 (2025).

Supplement E7. Ridge without rock shelter in the Chasseral (central Jura).

Anhang E7. Grat ohne Felsüberhang im Chasseral (zentraler Jura).



Ridge without rock shelter, east of the Chasseral anticlinal coomb (central Jura, 1595 m asl). The stratigraphic profile shows no “transitional formation”, in contrast to Nardaran (see Fig. 1, 2, 3, 5). The geological context and the resulting geomorphological complex therefore does not allow the formation of rock shelters and there is no underlying scree either due to the lack of vacuum. The nitrophilous vegetation is absent due to the lack of dung deposits (chamois or other) and the pasture (100% cover) extends to the foot of the ridge, with the presence of *Deschampsia caespitosa*, *Alchemilla vulgaris*, *Adenostyles glabra*, *Saxifraga rotundifolia*, etc. (Photo F. Béguin, 18.09.2023).

