

Geographic distribution and new localities for cryptic species of the *Aneura pinguis* complex and *Aneura maxima* in Poland

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Abstract: The genus *Aneura* is represented in Poland by two species – *A. pinguis* and *A. maxima*. *A. pinguis* in contrast to *A. maxima* is a complex of cryptic species temporarily named *A. pinguis* species: A, B, C, and E. All species of the *A. pinguis* complex and *A. maxima* differ in their geographic distribution and habitat preferences. *A. pinguis* species A grows mainly on humus over limestone rocks in the Western Carpathians, *A. pinguis* species B occurs mainly on clay soil in Bieszczady Mts. and in clayish areas of lowlands, *A. pinguis* species C grows both in lowlands and mountains and it occupies mostly wet sandy soils, on the shores of oligotrophic lakes and river and mountain stream banks, *A. pinguis* species E is connected with calcareous rocks in flowing water in mountains. *A. maxima* grows over the country – both in lowlands and mountains, in marshes situated on the river banks.

Key words: Bryophyta, thalloid liverwort, ecological preferences, pattern of geographic distribution

1. Introduction

The application of isozyme and molecular techniques to taxonomical studies in bryology resulted in the identification of cryptic species complexes within widespread bryophytes (e.g. Szweykowski & Krzakowa 1979; Boisselier-Dubayle & Bischler 1989; Shaw 2000; Feldberg *et al.* 2004; Hedenäs & Eldenäs 2007; Fuselier *et al.* 2009; Kreier *et al.* 2010; Heinrichs *et al.* 2010, 2011; Sawicki & Szczecińska 2011; Carter 2012). Cryptic species are characterized by the absence or almost absence of morphological differentiation, but the presence of significant genetic differentiation and reproductive isolation (Mayr 1970). Many studies indicated that genetic distances between cryptic species of liverworts are as large as between many species of vascular plants (e.g. Zieliński 1987; Dewey 1989; Bączkiewicz *et al.* 2005; Bączkiewicz & Buczkowska 2016). Before the discovery of cryptic species, many authors thought that slight morphological differences within these species were attributed to their plasticity (Szweykowski 1982). The reason for this is a simple morphology of thallus in liverworts and often the absence of distinct features that allow to identify species. This is the situation for

the thalloid liverwort species of *Aneura pinguis* (L.) Dumort.

A. pinguis sensu lato has a broad austral-tropical-arctic distribution – it grows in Europe, Asia, Australia, New Zealand, North America and Mexico (Paton 1999; Damsholt 2002). In Poland, it is locally common and known both from lowlands and mountains (Szweykowski 2006). It grows in various habitats: on calcareous rocks, basic humus, peat bogs, wet sand on lake shores and fallen decorticated logs (Szweykowski 2006). Until the end of the 20th century, *A. pinguis* was regarded as a morphologically homogeneous species in the whole range of its distribution, but recent genetic and chemotaxonomic studies revealed five cryptic species within *A. pinguis*, which were temporarily named *A. pinguis* species: A, B, C, D and E (e.g. Bączkiewicz & Buczkowska 2005, 2016; Wachowiak *et al.* 2007; Bączkiewicz *et al.* 2008; Wawrzyniak *et al.* 2014). Four of them (A, B, C and E) have so far been detected in Central Europe and D – on the British Isles (Bączkiewicz & Buczkowska 2005, 2016). All species of *A. pinguis* complex differ in their geographic distribution in Poland. Species A and E occur mainly in mountain areas, while species B and C are

Table 1. Localities of cryptic species of the *Aneura pinguis* complex (species B and C) and *A. maxima* (M) in the NW region of Poland with the number of sampled colonies and habitat characteristics

Region and Locality	Geographic coordinates	Elevation (m a.s.l.)	Soil	Species	No. of colonies
WL, Gosań Mt, on a cliff	N53°57' E14°30'	76	sandy soil with	B	1
WL, Cliff between Gosań and Świdna Kępa Mt.	N53°57' E14°29'	2	humus	B	1
WL, Świdna Kępa Mt, on a cliff	N53°57' E14°29'	35	humus	B	3
WP, Lake Książę near Kościerzyna	N54°05' E17°57'	203	humus	B	12
WP, Lake Małe Sitno near Czarna Dąbrówka	N54°16' E17°31'	111	humus	B	1
WP, Słupia river, on the bank of the river	N54°15' E17°29'	106	humus	B	3
WR, Kopanina, south-western part of Poznań	N52°38' E16°85'	90	clay soil	B	1
WR, Lakeland Wałeckie, Diabli Skok Reserve	N53°23' E16°34'	103	humus	B	3
WP, Lake Garczyn near Kościerzyna	N54°07' E17°54'	147	humus	C	6
WP, Lake Kulkówko near Kościerzyna	N54°04' E17°51'	143	sandy soil	C	1
WP, Słupia river, on the bank of the river	N54°15' E17°29'	97	humus	C	2
WR, Lakeland Wałeckie, Diabli Skok Reserve	N53°23' E16°34'	70	rotten wood	C	4
WP, Słupia river, on the bank of the river	N54°15' E17°29'	110	humus	M	2
WR, Lakeland Wałeckie, Diabli Skok Reserve	N53°23' E16°34'	78	humus	M	5

Explanations: WL – Wolin Island, WP – Western Pomerania, WR – Wielkopolska Region

present both in lowlands and mountains (Bączkiewicz & Buczkowska 2016). In Poland, also another species of the genus *Aneura* – *A. maxima* (Schiffn.) Steph, was found. This species can be easily distinguished from *A. pinguis* based on morphological traits. In Europe, *A. maxima* was found for the first time in Belgium in 1994 (Andriessen *et al.* 1995) and in Poland in 2002 (Buczkowska & Bączkiewicz 2006). Now, in Poland, the species is known from several localities.

We assumed that the samples of species from the genus *Aneura*, collected by the authors for over 13 years, may provide the basis for formulating general conclusions about geographic distribution of the studied *Aneura* species in Poland. Thus, the aim of this study was to show the pattern of geographic distribution of

cryptic species of the *A. pinguis* complex and *A. maxima* in Poland.

2. Material and methods

273 samples (colonies) of the *A. pinguis* complex (species A, B, C and E) and 23 samples of closely related species of *A. maxima* were collected from 11 regions of Poland (Tables 1-5). Localities of the genus *Aneura* were known from our earlier studies (e.g. Bączkiewicz and Buczkowska 2005, 2016; Buczkowska & Bączkiewicz 2006; Szweykowski 2006; Wachowiak *et al.* 2007). Samples were collected during the years: 2002-2015. In each population, all found colonies were studied. Each collected sample was divided into

Table 2. Localities of cryptic species of the *Aneura pinguis* complex (species: A, B, C) and *A. maxima* (M) in the NE region of Poland with the number of sampled colonies and habitat characteristics

Region and Locality	Geographic coordinates	Elevation (m a.s.l.)	Soil	Species	No. of colonies
BF, Żebra Żubra Reserve	N52°71' E23°80'	165	humus	A	1
ML, Lake Redykajny near Olsztyn	N53°81' E20°41'	120	humus	B	1
SLD, Lake Pierty east of Suwałki	N54°10' E23°09'	133	humus	B	1
SLD, Lake Druce north of Sejny	N54°15' E23°39'	139	humus	B	2
BF, Żebra Żubra Reserve	N52°71' E23°80'	160	humus	B	7
ML, Lake Ruskie near Ostruda	N53°83' E19°96'	115	humus	C	3
SLD, Lake Stulpień east Giby	N54°03' E23°46'	138	rotten wood	C	3
SLD, Lake Chylinki near Sejny	N53°96' E23°29'	134	rotten wood	C	1
BF, Żebra Żubra Reserve	N52°71' E23°80'	168	humus	C	1
ML, Lake Redykajny near Olsztyn	N53°81' E20°41'	120	boggy area	M	2
BF, Wysokie Bagno Reserve	N52°69' E23°89'	156	boggy area	M	6
BF, Żebra Żubra Reserve	N52°71' E23°80'	165	boggy area	M	2

Explanations: BF – Białowieża Forest, ML – Masurian Lakeland, SLD – Suwałki Lake District

Table 3. Localities of cryptic species of the *Aneura pinguis* complex (species A, B and C) and *A. maxima* (M) in the Bieszczady Mts with the number of sampled colonies and habitat characteristics

Locality	Geographic coordinates	Elevation (m a.s.l.)	Soil	Species	No. of colonies
Valley of Terebowiec stream	N49°06' E22°41'	772	humus	A	5
Górna Solinka Valley	N49°06' E22°31'	762	clay soil	B	4
Valley of Beskidnik stream	N49°06' E22°29'	775	clay soil	B	4
Valley of Terebowiec stream	N49°06' E22°41'	781	clay soil	B	2
Tributary of Wołosaty stream	N49°07' E22°40'	655	clay soil	B	4
Old quarry beside the road Brzegi Górne and Nasiczne	N49°09' E22°34'	708	clay soil	B	3
Ustrzyki Górne, small stream	N49°05' E22°38'	734	clay soil	B	6
Sianki, Niedźwiedzi stream	N49°01' E22°88'	725	clay soil	B	2
Górna Solinka Valley	N49°07' E22°29'	712	sandy soil	C	4
Ustrzyki Górne, small stream	N49°05' E22°38'	735	sandy soil	C	6
Valley of Terebowiec stream	N49°06' E22°40'	732	boggy area	M	3
Ustrzyki Górne, small stream	N49°05' E22°38'	732	boggy area	M	1

two parts. The first part was deposited as a voucher in the POZW herbarium, the second part was used for genetic identification of *A. pinguis* cryptic species. Genetic identification was based on an isozyme pattern

according to Bączkiewicz & Buczkowska (2016) and DNA sequences (Wachowiak *et al.* 2007). *A. maxima* was identified morphologically according to Furuki (1991) and Buczkowska & Bączkiewicz (2006).

Table 4. Localities of cryptic species of the *Aneura pinguis* complex (species A, B, C and E) and *A. maxima* (M) in the Tatra Mts. with the number of sampled colonies and habitat characteristics

Locality	Geographic coordinates	Elevation (m a.s.l.)	Soil	Species	No. of colonies
Valley of stream Biały Potok	N49°16' E19°57'	883	humus over	A	10
Jaworzynka Valley	N49°15' E20°00'	1432	limestone rocks	A	3
Olczyńska Valley	N49°16' E19°59'	1005		A	3
Pańszczyca Valley	N49°15' E20°02'	1422		A	3
Strążyska Valley	N49°16' E19°55'	993		A	6
Sucha Woda Valley	N49°16' E20°01'	1159		A	2
Kozieniecki Żleb gully	N49°27' E19°82'	1050		A	2
Krowi Żleb gully	N49°16' E20°01'	1030		A	4
NE slope of Skupinów Uplaz Mt	N49°15' E19°59'	1202		A	20
Sucha Wielka Valley	N49°27' E19°83'	980		A	2
Wąwóz Kraków gorge	N49°24' E19°87'	1250		A	4
Białka Valley	N49°26' E20°10'	1115	humus mixed	B	1
Valley of Biały Potok stream	N49°16' E19°57'	1002	with clay	B	2
Sucha Woda Valley	N49°16' E20°01'	1180		B	2
Valley of Biały Potok stream	N49°16' E19°57'	997	humus over	C	1
Pańszczyca Valley	N49°15' E20°02'	1403	limestone	C	3
Jaworzynka Valley	N49°15' E20°00'	1440	rocks	C	1
Sucha Woda Valley	N49°16' E20°01'	1160	sandy soil	C	3
NE slope of Skupinów Uplaz Mt	N49°15' E20°00'	1235		C	3
Valley of Biały Potok stream	N49°16' E19°57'	924	limestone rocks	E	15
Pańszczyca Valley	N49°15' E20°02'	1420	in flowing	E	9
Sucha Wielka Dolina Valley	N49°27' E19°82'	1030	water	E	2
Białka Valley	N49°26' E20°10'	1010	marsh	M	1
Olczyńska Valley	N49°16' E19°59'	990		M	1
Rów Zakopiański at N foot of Tatra Mts, Las Capowski forest	N49°17' E20°02'	973		M	1
Rów Zakopiański at the N foot of Tatra Mts, Chowańcówka stream	N49°17' E20°01'	1010		M	1

Table 5. Localities of cryptic species of the *Aneura pinguis* complex (species A, B and E) and *A. maxima* (M) in the Beskid Sądecki (BS), Małe Pieniny (MP) and Pieniny Mts (P) with the number of sampled colonies and habitat characteristics

Locality	Geographic coordinates	Elevation (m a.s.l.)	Soil	Species	No. of colonies
BS, Potok Kozlecki stream	N49°27' E20°27'	590	humus over	A	8
BS, Potok Szczawa stream	N49°27' E20°26'	514	detritus	A	14
BS, Potok Ścigocki stream	N49°25' E20°26'	447	flysch rocks	A	1
BS, Potok Wądołowy stream	N49°27' E20°26'	544		A	5
BS, Potok Wygon stream	N49°26' E20°26'	506		A	4
BS, Potok Podlipowiec stream	N49°46' E20°44'	620	humus	A	1
BS, Potok Kozlecki stream	N49°26' E20°26'	483	clay soil	B	2
BS, Potok Kozlecki stream	N49°28' E20°21'	525	marsh	M	2
MP, tributary of Potok Skalskie stream	N49°24' E20°33'	578	humus over	A	4
MP, Reserve of Potok Skalskie stream	N49°23' E20°33'	651	detritus	A	5
MP, Repowa Mt	N49°23' E20°33'	625	flysch rocks	A	1
P, Kotłowy Potok stream	N49°24' E20°24'	650		A	1
P, Barbarzyna	N49°25' E20°20'	580	humus	A	5
P, Biały Potok stream	N49°25' E20°23'	580		A	3
P, Pieniński Potok stream	N49°25' E20°24'	678		A	1
P, Limbargowy Potok stream	N49°25' E20°21'	638		A	8
P, Ziemroska, small stream	N49°26' E20°24'	493		A	1
P, Kotłowy Potok stream	N49°24' E20°24'	650	clay soil	B	6
P, Limbargowy Potok stream	N49°25' E20°21'	638		B	1
P, Limbargowy Potok stream	N49°25' E20°21'	638	rocks in flowing water	E	4

3. Results

Distribution of cryptic species of the *A. pinguis* complex and *A. maxima* is presented in the maps (Figs. 1-4).

3.1. Geographic distribution of the *A. pinguis* complex

N-W Poland lowlands

In NW Poland, two species of this complex occur: B and C. Species B is a representative of *A. pinguis*

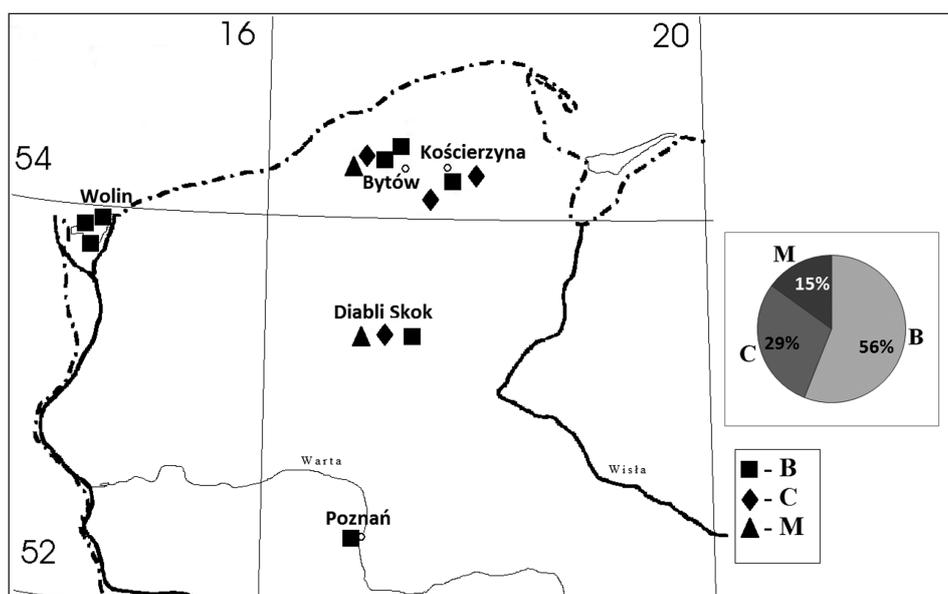


Fig. 1. Distribution map of the cryptic species of *Aneura pinguis* complex and *A. maxima* in N-W Poland and the percentage of collected colonies for each studied species

Explanations: B – *A. pinguis* species B; C – *A. pinguis* species C; M – *A. maxima*

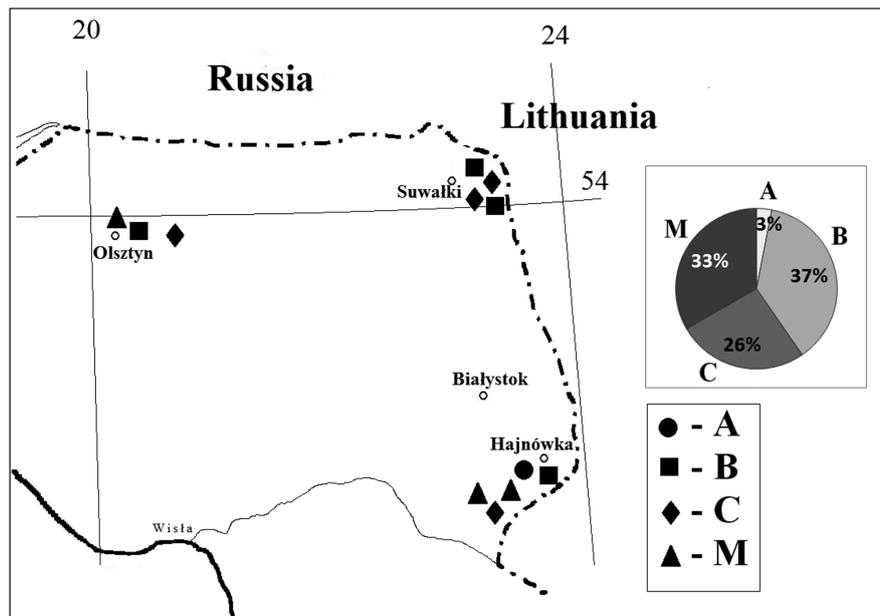


Fig. 2. Distribution map of the cryptic species of *Aneura pinguis* complex and *A. maxima* in N-E Poland and the percentage of collected colonies for each studied species

Explanations: A – *A. pinguis* species A; B – *A. pinguis* species B; C – *A. pinguis* species C; M – *A. maxima*

complex, which is most often found in lowlands. It was found in 8 localities. The number of colonies in these localities varied and ranged from 1 to 12. In total, 25 colonies of species B were found, i.e., 56% of all recorded colonies of the genus *Aneura* in this part of Poland. The rarer species C was noted only in the vicinity of Kościerzyna and Bytów (3 localities with 1-6 colonies) and in Wielkopolska – in the Diabli Skok reserve on the Rurzyca river (4 colonies). In total, 13 colonies of species C were found in this region of Poland (Fig. 1).

N-E Poland lowlands

In N-E Poland, all three species of *A. pinguis* complex were found: A, B and C (Fig. 2). Just like in N-W Poland, species B and C dominate. Both these species were found in 4 localities, in 3 regions of N-W Poland: Warmia-Mazury Lakeland, Suwałki Lakeland and Białowieża Forest. Similar to N-W Poland, species B is slightly more frequent than species C and forms larger colonies, with a higher number of thalli. In total, the species B colonies make 37% of all collected colonies of *A. pinguis* in this region. Contrary to N-W Poland, in N-E Poland also *A. pinguis* species A was found. The latter is very rare in lowlands. A single colony of this species was noted in the Białowieża Forest – a primeval forest, renowned for being an enclave of old European flora (e.g. Bobiec 2002; IOP PAN ed. 2006-2007; Korczyk 2008). Presently, it is a Biosphere Reserve (UNESCO 1980). Such old and persistent primeval forests are particularly vital for the preservation of flora in Europe.

They allow the survival of species with poor ability to colonize new sites, dependent on stable humidity and sensitive to air pollution (Faliński 1993; Klama 1995, 1996; Stewart 1995). In this part of Poland, many species still occur that disappeared from other regions or are very rare (e.g. Bobiec 2002; Korczyk 2008). They include also different species of liverworts that, outside the Białowieża Forest, are very rare in lowlands and occur only in the scattered, isolated localities, as forest relicts (Klama 2002).

Bieszczady Mts

The species composition of the genus *Aneura* in the Bieszczady Mts, which belong to the Eastern Carpathians, more resembles the Polish lowlands than the Western Carpathians. In Bieszczady, similar to the lowlands, *A. pinguis* species B dominates (Fig. 3). This species was found in 7 out of 10 localities with the species of *A. pinguis* complex. The proportion of species B colonies in this region was 57%. The second most abundant taxon was species C. The latter was found in 2 localities, where it formed 10 colonies. Also, a single locality of species A, with 5 colonies, was noted in Bieszczady, in the Terebowiec Valley.

The species composition of the genus *Aneura* in Bieszczady differs considerably from other mountain regions. This difference results from the various effects of Pleistocene glaciations on these regions. During glaciations, vegetation of Eastern Carpathians could easily migrate towards the Balkan Peninsula, thus, its survival rate was higher than in other regions of Poland

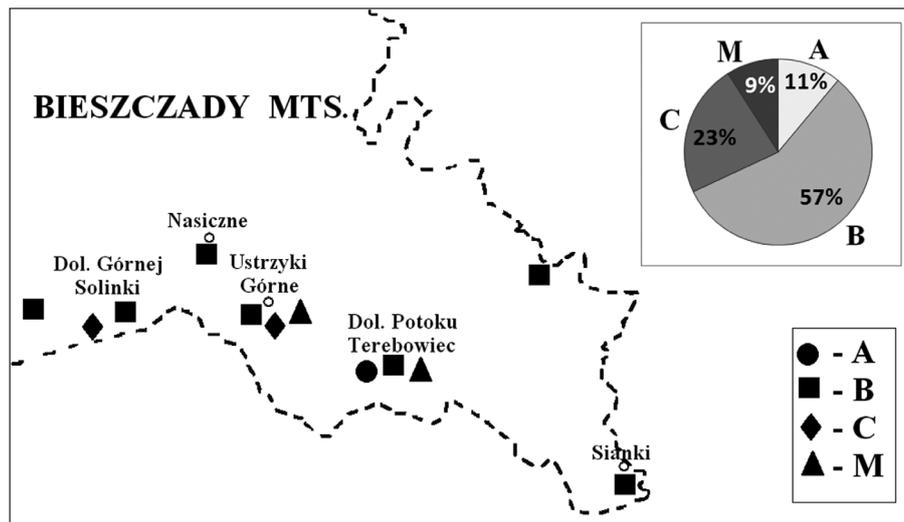


Fig. 3. Distribution map of the cryptic species of *Aneura pinguis* complex and *A. maxima* in the Bieszczady Mts and percentage of collected colonies for each species

Explanations: A – *A. pinguis* species A; B – *A. pinguis* species B; C – *A. pinguis* species C; M – *A. maxima*

(Pawłowski 1972). The differences in species composition may be noticed also in other liverworts – some hepatic species that are widespread and common in the Western Carpathians and Sudetes are either completely absent in the Eastern Carpathians or very rare (Szwedkowski & Buczkowska 1996).

Tatra Mts

In the Tatra Mts, the *Aneura* species occur mainly in the lower mountain zones (forest and montane zones)

(Fig. 4). The majority of localities occur in the N-E part of this range. All cryptic species of *A. pinguis*, i.e., A, B and C, known from the other area of Poland, occur also in Tatras. Species A had the highest number of localities (11), with several to several dozens of colonies. In total, the colonies of this species made 56% of all encountered colonies of *Aneura* species. The second most abundant species was species C. It was found in 5 localities, situated mainly in the central-west part of Tatras – in the Biały Potok and Sucha Woda Valleys. These localities

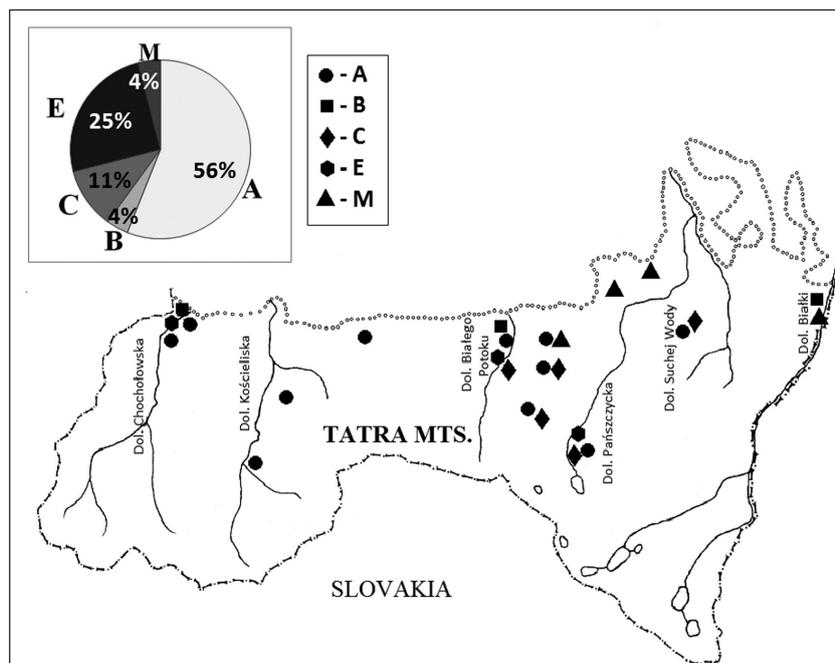


Fig. 4. Distribution map of the cryptic species of *Aneura pinguis* complex and *A. maxima* in the Tatra Mts and the percentage of collected colonies for each (cryptic) species

Explanations: A – *A. pinguis* species A; B – *A. pinguis* species B; C – *A. pinguis* species C; E – *A. pinguis* species E; M – *A. maxima*

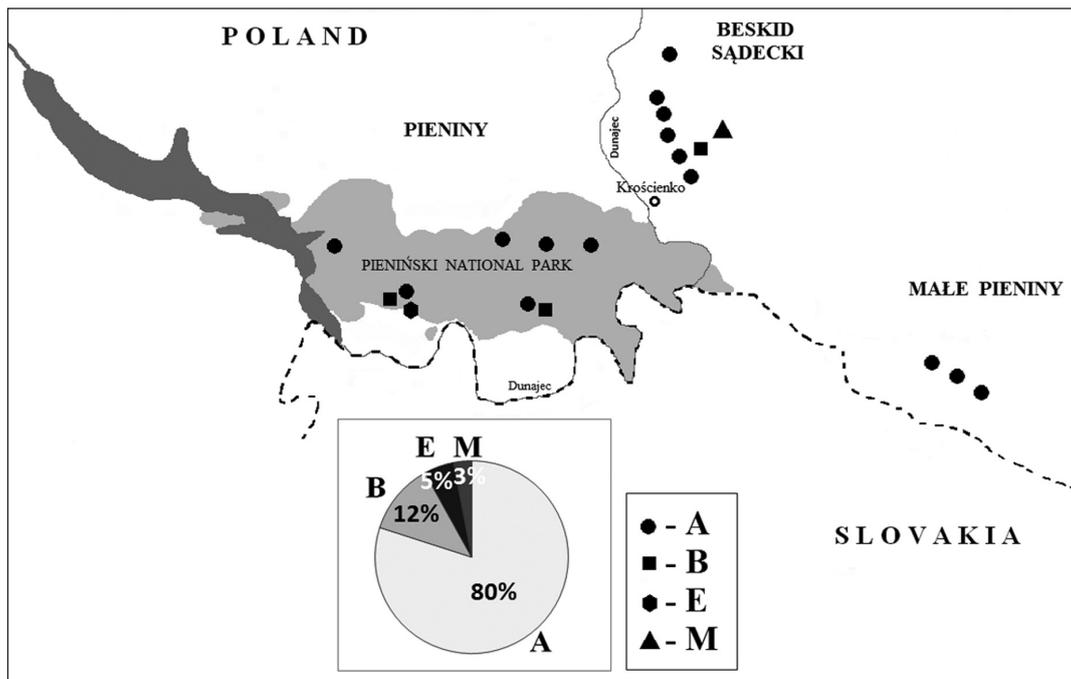


Fig. 5. Distribution map of the *Aneura pinguis* complex and *A. maxima* in the Pieniny, Male Pieniny and Beskid Sądecki Mts and the percentage of collected colonies for each (cryptic) species
 Explanations: A – *A. pinguis* species A; B – *A. pinguis* species B; E – *A. pinguis* species E; M – *A. maxima*

comprised a small number of colonies (1-3), which, in total made 11% of all recorded colonies in this region. The colonies were small in size, which is characteristic for this species. The recent investigations of *A. pinguis* complex in Poland revealed one additional species – species E (Wawrzyniak *et al.* 2014). In the Tatra Mts, it was found in 3 localities with 2-15 colonies. These colonies made 25% of all *Aneura* colonies found in the Tatra Mts and were large and dense. In Bieszczady and lowlands, this species does not occur. Possibly, this may result from its habitat preferences – it grows only on calcareous rocks in flowing water. Such habitats are very rare in lowlands and Bieszczady. The rarest species of *A. pinguis* complex in Tatra was species B. Its small colonies were found only in 3 localities – in the Białka, Biały Potok and Sucha Woda Valleys.

Pieniny, Small Pieniny and Beskid Sądecki Mts

The Pieniny, Small Pieniny and Beskid Sądecki Mts, together with the Tatra Mts, form the eastern part of Western Carpathians. Localities with as much as 3 species of *A. pinguis* complex (A, B and E) were found in these mountain ranges (Fig. 5). The border between the Eastern and Western Carpathians goes between the Beskid Niski (which lies next to the Beskid Sądecki) and Bieszczady Mts through the Łupków Pass. The vegetation of the Beskid Niski and Sądecki Mts has a transitory character – both the Western and Eastern

Carpathian species are present (Pawłowski 1972). This concerns also the species of *A. pinguis* complex. On one hand, in the Western Carpathians, similarly like in Tatra, species A prevails. It was found in 15 out of 20 localities of *Aneura* species (6 localities in Pieniny and Beskid Sądecki each and 3 in Small Pieniny; in the latter, it is only representative of the *A. pinguis* complex). The colony number of this species in individual localities ranged from 1 to 14. In total, 62 colonies were found, i.e. 80% of all collected colonies of the genus *Aneura* in this region. On the other hand species E, almost exclusively limited to Tatra, was found also on the Limbargowy Stream in Pieniny, where it formed 4 large colonies, but in Beskid Sądecki was absent. Moreover, 3 localities of species B, characteristic for lowlands and Bieszczady, were found with the occurrence frequency of 12%, while species C, which was present in other regions – particularly, in lowlands and Bieszczady, was absent in this area.

3.2. Geographic distribution of *A. maxima*

A. maxima, the second species of the genus *Aneura* occurring in Poland, was found all over the country – both in lowlands and mountains. This species is associated with a characteristic type of a habitat – marshes situated on the river banks, where it usually colonizes the whole available boggy area, forming large colonies (much larger than in case of *A. pinguis*), often ranging from a few to up to 20 m² in size, which is

Table 6. The occurrence percentage of species of the *Aneura pinguis* complex and *A. maxima* in the studied regions of Poland

Regions	% of occurrence of species of the <i>A. pinguis</i> complex and <i>A. maxima</i>				
	A	B	C	E	M
N-W POLAND LOWLANDS	0	33.3	31.0	0	25.9
Wolin Island	0	6.7	0	0	0
Western Pomerania	0	21.3	21.5	0	7.4
Wielkopolska	0	5.3	9.5	0	18.5
N-E POLAND LOWLANDS	0.8	14.6	19.0	0	37.1
Masurian Lakeland	0	1.3	7.1	0	7.4
Suwałki Lake District	0	4.0	9.5	0	0
Białowieża Forest	0.8	9.3	2.4	0	29.7
EASTERN CARPATHIANS	3.9	33.3	23.8	0	14.8
Bieszczady Mts	3.9	33.3	23.8	0	14.8
WESTERN CARPATHIANS	95.3	18.7	26.2	100.0	22.2
Tatra Mts	46.4	6.7	26.2	86.7	14.8
Beskid Sądecki Mts	26.0	2.7	0	0	7.4
Małe Pieniny Mts	7.9	0	0	0	0
Pieniny Mts	15.0	9.3	0	13.3	0

characteristic for this species. 4 localities of *A. maxima* were found in the Polish lowlands (Figs. 1-2), 2 in Bieszczady (Fig. 3), 4 in Tatras (Fig. 4), and 1 in Beskid Sądecki (Fig. 5). The highest number of colonies (17) was noted in lowlands, i.e., 7 in N-E and 10 in N-W Poland, which made 33% of all found colonies of the genus *Aneura* in this region. 7 colonies of *A. maxima* were recorded in the vicinity of Bytów, on the Słupia river and in the Diabli Skok reserve.

4. Conclusions

A detailed analysis of the distribution pattern of representatives of the genus *Aneura* in Poland was conducted and a clear association between the individual species occurrence and type of habitat was observed.

The cryptic species of the *A. pinguis* complex prefer wet, alkaline habitats, such as: limestone rocks, humus over lime rocks, shales or clay (Tables 1-5). The occurrence of individual *A. pinguis* species in different regions of Poland varies, which, presumably, results from different habitat preferences (Table 6). The highest habitat diversification is in Tatras, thus, all *A. pinguis* species were found in this region. This is due to the conducive climatic conditions for growing liverworts and a large variety of soil. Species A, which grows mainly on humus over limestone rocks, is characteristic for the Western Carpathians. Species B occurs mainly on clay soil and it dominates in Bieszczady, where this type of soil prevails, and in clayish areas of lowlands. Species C occupies mostly wet sandy soils, e.g., on the

shores of oligotrophic lakes and river and mountain stream banks, hence, it is present both in lowlands and mountains. Species E is connected with calcareous rocks in flowing water. The highest number of this type of localities occurs in the Western Carpathians, which is possibly the cause of the species presence only in this region.

The observed pattern of distribution of *A. pinguis* species indicates that cryptic speciation in *A. pinguis* possibly results from the specialization in adaptation to habitat. Individual cryptic species may grow in direct proximity in a given area, but still form separate colonies, e.g., in Tatras – species A and C in the Sucha Woda Valley, A and E in the Pańszczyca and Biały Potok Valleys, while in Bieszczady – species B and C in the Górna Solinka Valley, which, probably, is the result of a high soil diversification in these areas.

In turn, *A. maxima* has more localities in the lowlands of Poland than in the mountain regions (Tables 1-5). Similarly like in case of cryptic species of *A. pinguis* complex, this distribution results from the specific habitat preferences of *A. maxima*, i.e., swampy soils along the banks of rivers (Table 6).

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