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CONTRIBUTION ON THE LEMNACEAE OF ECUADOR

ELIAS LANDOLT

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ABSTRACT: In August 1999, a field trip through different regions of Ecuador was undertaken, and distribution and ecology of the various species of Lemnaceae were studied. Fourteen species were found: *Spirodela intermedia* W. Koch, *S. polyrrhiza* (L.) Schleid., *Landoltia punctata* (G. F. W. Meyer) Les & Crawford [*Spirodela punctata* (G. F. W Meyer) Thompson], *Lemna gibba* L., *L. obscura* (Austin) Daubs, *L. aequinoctialis* Welw., *L. valdiviana* Phil., *L. minuta* H. B. K., *Wolffiella welwitschii* (Hegelm.) Monod, *W. lingulata* (Hegelm.) Hegelm. *W. oblonga* (Phil.) Hegelm., *Wolffia brasiliensis* Weddell, *W. columbiana* Karsten, and *W. globosa* (Roxb.) den Hartog & van der Plas. *Landoltia punctata*, and *Wolffia globosa* were recorded in Ecuador for the first time. The only visited area in the Amazon region (Cuyabeno Lake) was void of Lemnaceae due to very low nutrient content of the water. In the central region of the Andes, standing waters are rather rare. *Lemna gibba*, *L. minuta*, *L. valdiviana*, *Wolffia brasiliensis*, and *Spirodela intermedia* were observed. Only rarely were the wet rocks of the west side of the Andes covered by fronds of *L. valdiviana* s.l. The coastal region between Esmeraldas and Machala proved to be especially rich in Lemnaceae. An unexpected high frequency of *S. polyrrhiza* was observed. About 50 relevés of pleustonic communities were recorded and grouped in various vegetation units.

KEY WORDS: distribution, duckweeds, Ecuador, Lemnaceae, pleustonic vegetation

E. Landolt, Geobotanisches Institut ETHZ, Zürichbergstr. 38, CH–8044 Zürich, Switzerland

INTRODUCTION

Since nearly 50 years, the present author has studied the biology of the monocotyledoneous family of the Lemnaceae. This family was investigated during many trips to various areas of all continents. On one of these trips through Argentina (1983), the author was accompanied by Kazimierz Zarzycki. We studied the wetland vegetation of Central and Northern Argentina for three weeks, collecting Lemnaceae samples, measuring water qualities and discussing the relationship between environmental conditions and the occurrence of water vegetation. Kazik was an ideal companion and collaborator, always good-humoured, interested, persevering, and patient. I have a wonderful and impressive memory of that excursion. I am glad to dedicate some of my results of a similar Ecuadorian trip to Kazik on occasion of his seventieth birthday.

The Lemnaceae flora of South America has not been well investigated until recently. The distribution and ecology of the members of this family was only known fragmentarily. Borhidi *et al*. (1979, 1983) published relevés of aquatic vegetation from Cuba. The

Lemnaceae vegetation has been included mainly in one alliance (*Azollaeo-Salvinion* Borhidi & Muniz 1979) of the order *Salvinio-Eichhornietalia* Borhidi 1979 and the class *Salvinio-Eichhornietea* Borhidi & Del Risco 1979. The two associations (*Lemno-Azolletum carolinianae* Borhidi & Muniz 1979 and *Salvinietum auriculatae* Borhidi & Muniz 1979) consist of three species (the authors cite *Lemna perpusilla* Torrey and *L. trinervis* Small which are identical with *L. aequinoctialis* Welw., *Spirodela polyrrhiza* (L.) Schleid. and *Azolla caroliniana* Willd.) and five species (*Salvinia auriculata* Aubl., *S. rotundifolia* Willd., *Lemna perpusilla* which is called today *L. aequinoctialis*, *Spirodela polyrrhiza*, *Pistia stratiotes* L.), respectively. In the individual relevés only two or three species were noted. Interestingly, no *Wolffiella* (Hegelm.) Hegelm. species was observed though, *W. lingulata* (Hegelm.) and *W. welwitschii* (Hegelm.) Monod. are known from Cuba. The relevés represent just fragments of wide-spread Lemnaceae combinations. It is not possible to integrate them in one of the associations referred to in the following chapters. Müller and Gutte published 1985 results of phytsociological investigations on aquatic vegetation of the coast region of Central Peru. They distinguished three associations: the *Eichhornia crassipes-Pistia stratiotes* unity, the *Azolla filiculoides-Lemna valdiviana* unity, and the *Wolffia columbiana-Lemna gibba* unity. Provided that the identifications are correct, the unities belong into the alliance *Azollo filiculoides-Lemnion gibbae* of Landolt 1999 and near the *Lemno minutae-Lemnetum gibbae* Liebermann Cruz *et al*. 1988 and the *Azollo filiculoides-Wolffielletum oblongae* Landolt 1999. It is remarkable that Müller and Gutte did not note *Wolffiella* species in the coastal region of Peru. In coastal regions of most other countries of South America various species of this genus are frequent. Eskuche (1986) was the first to present some accurate and complete relevés of Lemnaceae vegetation in lowland South America. Extensive indications of the ecology and distribution of the various Lemnaceae species in Argentina are given in Landolt and Zarzycki (1994). Landolt (1999) presents a survey of South American Lemnaceae vegetation. However, information over large geographic areas is still missing. To fill out one of this gaps a trip to Ecuador was undertaken in July 1999 together with E. Terneus and W. Lämmler.

Study area and field measurements

The location of the 72 investigated water sites in Ecuador are shown in Fig. 1 and Table 1. On the whole, three regions were visited: *(1)* the central region of the Andes between the surroundings of Riobamba in the South and Ibarra in the North; *(2)* the Amazon region in the Cuyabeno area, and *(3)* The Coastal region between Naranjal in the South and Esmeraldas in the North.

Ecuador is situated along the equator line. The climate of the three regions is presented in Fig. 2. For the whole country, the climate is characterized by very low variation between mean monthly temperatures throughout the year. Fig. 3 shows the isographs of the aridity factor of Martonne. This factor *i* represents the relation between precipitation and temperature:

Fig. 1. Visited localities and origines of the relevés (see Table 1).

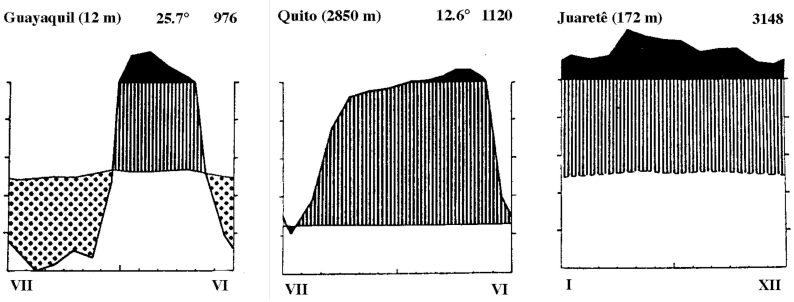

Fig. 2. Climate diagrams of three different stations corresponding to the three visited regions in Ecuador (from Walter & Lieth 1967): a – Guayaquil, representing the climate of the Coastal region; b – Quito, representing the climate of the central region of the Andes; c – Juaretę (Brazil) representing the climate of the Amazon region.

$$i = \frac{\text{precipitation (in cm)}}{\text{mean annual temperature in } (^{o}\text{C}+10)} .$$

Lemnaceae grow generally only between the values of 1 and 8 (see Table 2).

In the valleys of the central region of the Andes between 2200 and 2850 m, the climate is warm temperate (mean temperatures between 12 and 15°C) and sunny, with

Table 1. Localities of collected Lemnaceae and investigated water samples.

No.	Locality
1–3	Imbabura, Laguna San Pablo, 2670 m.
4–5	Imbabura, Lago de Yaguacocha, 2195 m.
6	Pichincha, Rio Chiche between Pito and Tumbaco, 2250 m.
7–9	Chimborazo, Laguna de Colta, 3280 m.
10	Chimborazo, between Riobamba and Ambato, 3480 m.
11	Tungurahua, Laguna de Yambo, 2580 m.
12	Pichincha, Napa waterfall between Tandapi and San Domingo, 1000 m.
13	Pichincha, Tandapi, below a rock wall, 1480 m.
14	Pichincha, between Tandapi and Aloag, 2600 m.
15–17	Sucumbíos, Laguna Cuyabeno.
18	Sucumbíos, Lago Agrio, Airport.
19	Esmeraldas, La Y de la Laguna.
20	Esmeraldas, Viche, San Nicolas.
21–23	Esmeraldas, S of Esmeraldas.
24–25	Esmeraldas, surroundings of Atacames.
26–28	Esmeraldas, between Súa and El Salto.
29	Manabí, SW of El Carmen.
30	Manabí, Lago de Rosario.
31	Manabí. Estero Seco.
32–37	Manabí, surroundings of Pedernales.
38–39	Manabí, surroundings of Jama
40	Manabí, junction San Vicente – Chone / Bahia – Chone.
41–48	Manabí, surroundings of Chone.
50–52	Manabí, E of Rocafuerte.
53	Manabí, S of Jipijapa.
54–55	Guayas, Zamora Nueva.
56–61	Guayas, surroundings of Novol.
62	Guayas, Pascuales.
63	Guayas, E of Duran.
64–65	Guayas, surroundings of Gral. Pedro J. Montera.
66	Guayas, W of Triunfo.
67	Guayas, NE of Duran.
68–70	Guayas, surroundings of Yaguachi Nuevo.
71	Los Ríos, S of Babahoyo.
72	Los Ríos, S of Patricia Pilar.

a rather dry period between June and August, and a more wet period between October and May. The mean annual precipitation varies between 1000 and less than 500 mm.

The area is intensely cultivated, and the natural vegetation is greatly reduced. The few forests consist of planted *Eucalyptus* and of *Pinus radiata* trees. The outer steep slopes of the Andes are provided with high precipitation and high air humidity throughout the whole year and are covered by tropical mountain rain forest.

In the Amazon region, a typical lowland rain forest climate is prevalent, with mean temperature between 20°C in the West and 26°C in the East. Mean annual rainfall amounts to between 2000 and 6000 mm. The months of April to June are wetter each than the other months of the year. The region is in general rather sparsely populated, and forests are still widespread.

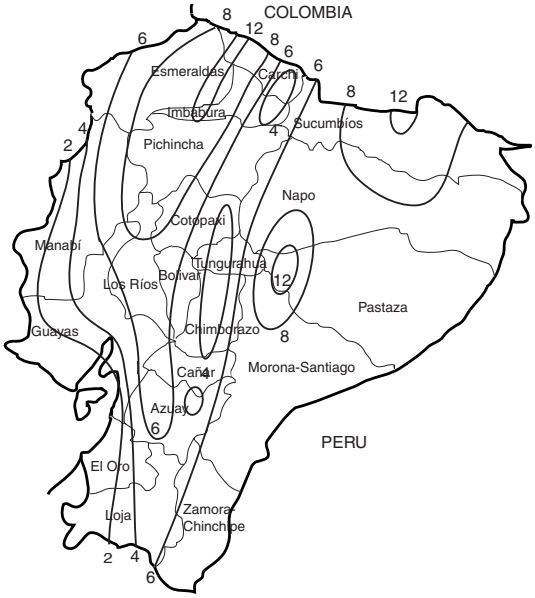

Fig. 3. Isographs of the aridity factor of Martonne within Ecuador.

Table 2. Climatic parameters which limit the distribution of Ecuadorian Lemnaceae (after Landolt 1986, modified)*. 1 – lowest mean temperature of the three coolest months in °C; 2 – lowest absolute minimum temperature in °C; 3 – highest mean temperature in °C of the three warmest months; 4 – lowest mean temperature in °C of the three warmest months; 5 – aridity factor of Martonne: annual precipitation in cm divided by the mean annual temperature + 10 °C.

Species	Climate characteristics				
	1	2	3	4	5
Spirodela intermedia	8	-10	> 28	14	3–8
S. polyrrhiza	-40	< -40	> 28	16	2–8
Landoltia punctata	1	-10	28	10	5–8
Lemna gibba	-1	-20	26	10	1–4
L. obscura	-1	-20	28	18	3–6
L. aequinoctialis	8	-20	> 28	20	1–8
L. valdiviana	-1	-20	> 28	12	4–8
L. minuta	-1	-20	26	12	2–6
Wolffiella welwitschii	18	> 0	> 28	25	2–5
W. lingulata	8	-8	> 28	15	2–8
W. oblonga	8	-10	28	13	2–6
Wolffia brasiliensis	-1	-20	28	13	2–5
W. columbiana	-12	-20	28	15	2–5
W. globosa	1	-20	>28	22	3–6

* In comparison to the indication in Landolt (1986) a few values have been slightly modified. Especially the values for lowest mean temperature of the three warmest months had to be lowered for *Spirodela intermedia*, *Lemna minuta*, *Wolffiella lingulata*, *W. oblonga*, *Wolffia brasiliensis*, and *W. columbiana* according to observations made in tropical regions at higher altitudes. Also, the span of Martonne factor was reduced for *Landoltia punctata* and *Wolffia globosa*, and enlarged for *Wolffiella oblonga*.

The mean temperature of the coastal region vary mostly between 23 and 26°C. The precipitation increases from less than 500 mm in the Southwest to 5000 mm in the Northeast. The rainy season is between January and April. However, the days are also very often cloudy or foggy in the dry season. Most of the region is densely populated and intensely cultivated, though some areas within the coastal mountains are still covered with natural vegetation which consists of desert, semidesert, dry deciduous to humid semideciduous forest, according to the amount of rainfall.

On each visited locality the pleustonic vegetation was analysed and pH and conductivity measured. Vouchers of Lemnaceae samples are deposited in QCA and ZT. Acronyms of herbaria follow Holmgren *et al.* (1990).

Specimens of Ecuadorian Lemnaceae were checked in most of the bigger world herbaria. In addition I received material from T. Terneus, Quito and J. E. Madsen, Risskov, Denmark. In Ecuador, I looked through the herbaria QCA and GUAY.

Climate and distribution

Central regions of the Andes

Lemnaceae vegetation within the visited area is restricted to a few ponds and creeks, and some waterfalls of the western side of the Andes. Ponds are rare in this region, probably due to rather permeable soils. Esteban Terneus who studies the wetland vegetation did not know of any other water containing Lemnaceae in the visited area. Therefore, it can be assumed that we did not miss many places with duckweeds. The species in the Andes are the same as in other regions of similar altitudes, i.e. species which do not need high temperatures for good growth and which can withstand slight frosts (Table 2): *Spirodela intermedia* (rare), *Lemna gibba*, *L. minuta*, *L. valdiviana*, *Wolffiella oblonga*, and *Wolffia brasiliensis*.

The localities with Lemnaceae growing in standing or slowly flowing waters are situated between 2190 and 3280 m. *Lemna gibba* and *L. minuta* are restricted to this area because they cannot stand high temperatures for longer periods. *Wolffiella oblonga* can only be found occasionally outside of this region. It is able to tolerate slightly higher temperatures. *Spirodela intermedia* and *Lemna valdiviana* also grow frequently in the lowlands.

On three places along the road from Aloag to San Domingo, a *Lemna* similar to *L. valdiviana* was observed on steep rocks. The habitat is very much the same as the one of *L. yungensis* from Bolivia (Landolt 1998). It needs to be investigated further if the plants from Ecuador belong to this same taxonomic unit, if they should be incorporated under *L. valdiviana* s. str., or if they should form an endemic taxon of their own. It is possible that in other places on both sides of the Andes, rock duckweeds can be found in addition as well. The ecological requirements are: *(1)* rocks which are wet throughout the whole year, *(2)* nearly vertical walls, so that additional water during wet periods flows directly to the bottom of the rock and does not wash away the fronds, *(3)* high air

humidity and only occasional full sunshine, *(4)* no frost, and *(5)* not too low content of nutrients in the water. In the three investigated samples (nos. 12, 13, and 14 of Table 1) the conductivity of the water varied between 74 and 108 μS cm^{-1}. In Bolivia the values amounted to only 45–75 μS cm^{-1}. The altitudes of the three localities was 1000 m, 1480 m, and 2600 m, respectively.

Amazon region

In the Amazonian region, only the area between Lago Agrio and Laguna Cuyabeno was visited, where no members of the duckweed family were found. The precipitation is very high (between 3000 and 5000 mm per year) and the soils poor in nutrients. Around Cuyabeno Lake the water conductivity of three waters varied between 9 and 16 μS cm^{-1}. In a palm swamp at the airport of Lago Agrio, a conductivity of 78 μS cm^{-1} was measured. In general, the mineral and nutrient content of the waters in that region is far too low to maintain Lemnaceae growth.

Other areas of the Amazon region have precipitations of 2000 to 3000 mm per year. The approximate Martonne factor varies between 6 and more than 12. Lemnaceae are usually not found in areas with a factor higher than 8. The following Ecuadorian species grow in areas with factors between 6 and 8 (Table 2); therefore they can be expected in the region: *Spirodela intermedia, S. polyrrhiza, Lemna aequinoctialis, L. valdiviana, Wolffiella lingulata,* especially along some white-water rivers which originate in the Andes. However, the only collections of Lemnaceae from the Amazon region which I checked in herbaria originate from Pastaza, Rio Capihuari (76°50–55′W and 2°30–31′S) with *Spirodela intermedia* and *Lemna aequinoctialis* and from Napo, Ahuano and E of Coca with *S. intermedia.*

Coastal region

The Coastal region is rich in Lemnaceae. Only very wet areas in the Northeast as well as the desert and semidesert areas of the Southwest are rare in Lemnaceae vegetation. In general, Lemnaceae grow only in areas with a Martonne factor between 2 and 8 (Table 2). In addition, coastal mountains with permeable soils are poor in standing waters and, therefore, also in Lemnaceae.

Some species, such as *Lemna aequinoctialis, L. valdiviana, Wolffiella lingulata, Wolffia brasiliensis, W. columbiana,* and *Spirodela intermedia,* are distributed throughout most of South America under warmer temperature conditions. They are also wide-spread in the coastal area of Ecuador. In South America *Wolfiella welwitschii* is restricted to the warmest places in rather dry areas without frosts. Therefore, it is not found in the cooler areas of the South and of the Andes, as well as in the humid areas of the Amazon basin and parts of the eastern coast.

The rest of the species (*Spirodela polyrrhiza, Landoltia punctata, Lemna obscura,* and *Wolffia globosa*) have a restricted area in South America. *S. polyrrhiza* is known only from the Northwest, so far. From Ecuador, it was collected in 4 localities of the coastal

region. We found it in many places. It is by far more frequent than *S. intermedia*. The first herbarium collection dates back to 1923. It might well be that *Spirodela polyrrhiza* was introduced to South America, but could not spread further south and east due to the barriers of coastal deserts and mountain chains of the Andes. An introduction to South America is still more probable for *Landoltia punctata*. This species, better known under the name of *Spirodela punctata*, has been changed by Les and Crawford (1999) to a genus of its own. It was unknown in Ecuador until recently. In South America it is restricted to the East Coast between Sao Paulo and Rio de Janeiro. A sample from Orange Harbor, Tierra del Fuego, Chile, was collected in 1838, but was never found again since then. It is interesting to note that *Landoltia punctata* is localised in South America in the surroundings of harbours (Orange Harbor, Rio, Sao Paulo, Esmeraldas). In Ecuador it is today distributed in the northern and more humid part of the Coastal region, between Chones and Esmeraldas. In contrast, *Lemna obscura* grows in the southern and dryer part of the Coastal region, between Pascuales and Santa Rosa. The present general distribution of *L. obscura* encloses the southern states of the USA, the highland of Mexico, the northern part of Colombia and the coastal region of Ecuador. In Hawaii it is introduced. It cannot be excluded that the same is true for South America, too. The first collection from South America (between Machal and Santa Rosa) dates back to 1974. Landolt (1980) described the collection of this species from Ecuador as a new species, *L. ecuadoriensis*. Further studies of Ecuadorian and Colombian material revealed that *L. ecuadoriensis* is identical with *L. obscura*. Finally, *Wolffia globosa*, not recorded from Ecuador until now, is restricted in South America to northern Colombia and the Coastal region of Ecuador, similarly to *Lemna obscura*. The main distribution of this species is in southeastern Asia. The occurrences in the southern states of the USA and in Hawaii are believed to be of recent origine. It must be concluded that the species is also not native in South America. The species was first observed in South America in 1995 (Landolt 1999).

Species distribution in Ecuador

The distribution of each Lemnaceae species is summarized in Figs 4 to 10. Apart from the collected samples of our trip, the following herbarium specimens were identified.

Spirodela intermedia: Prov. Imbabura, Lago San Pablo (*Camp 3254*, 19.5.1945: S; *Fagerlind 1325 bis*, 18.11.1952; *Raimann*, 15.1.1992: ZT). Prov. Los Rios, Zapotal Nuevo, Carbo Malo (*Bonifaz 40*, 9.8.1981: GUAY). Prov. Manabí, 5 km E of Chone (*Bravo 41*, 12.8.1980: QCA, 15.8.1980: QCA). Prov. Napo, Anaconda near Ahuano (*Klötzli*, 12.1991; ZT); between Coca and Nueva Rocafuerte, Laguna de Añanza (*Raimann*, 27.5.1992: ZT). Prov. Pastaza, Rio Capihuari, 76° 50–55′ W, 2° 30–31′S (*Ollgard et al. 35062*, 23.7.1980: AAU, QCA).

Spirodela polyrrhiza: Prov. Esmeraldas, 25 km S of Esmeraldas (*Sparre 15451/52*, 12.4.1967: S). Prov. Guayas, Rio Macul (*Fagerlind 319A*, 29.9.1952); Milagro (*Hitchcock 20251*, 2.7.1923: GH, US); between Las Americas and Daule (*Fagerlind & Wibom 319*, 13.91952: UPS); Pedro J. Montero (*Bonifaz & Cornejo 3901*, 9.1.1999; GUAY); El Suspíro (*Cornejo & Bonifaz 6880*, 19.9.1999).

Lemna gibba: Prov. Imbabura, Lago San Pablo (*Asplund 7226*, 24.6.1939: R, UPS, US; *Camp 3254*, 19.5.1945: S; *Fagerlind 1325*, 18.11.1952: S); Lago de Cotalo (*Spruce 5064*, 1857: BM, C, G, GH, GOET, MO, STU). Prov. Chimborazo, Laguna de Colta (*Terneus et al. s.n.*, 20.3.1997: QCA).

Fig. 4. Distribution of ● *Spirodela intermedia* and ⋆ *Spirodela polyrrhiza* in Ecuador.

Fig. 5. Distribution of ⋆ *Landoltia punctata*, ● *Lemna gibba* and ▲ *Lemna obscura* in Ecuador.

Fig. 6. Distribution of ● *Lemna aequinoctialis* in Ecuador.

Fig. 7. Distribution of ● *Lemna valdiviana* and ⋆ *Lemna minuta* in Ecuador.

Fig. 8. Distribution of ● *Wolffiella welwitschii* and ⋆ *Wolffiella lingulata* in Ecuador.

Fig. 9. Distribution of ● *Wolffiella oblonga* and ⋆ *Wolffia globosa* in Ecuador.

Fig. 10. Distribution of ● *Wolffia brasiliensis* and ⋆ *Wolffia columbiana* in Ecuador.

Lemna obscura: Prov. Guayas, 10 km NE of Guayaquil (*Lüönd s.n.*, 20.11.1984: ZT) Prov. Oro, Machala – Santa Rosa (*Plowman et al.* 4609 2.12.1974; F, GH, U).

Lemna aequinoctialis: Prov. Esmeraldas, 25 km S of Esmeraldas (*Sparre 15451/52*, 12.4.1967: S). Prov. Guayas, Durán (*Asplund 5794*, 22.4.1939: S); between Guayaquil and Chongón (*Asplund 5232*, 8.3.1939: S); S of Engabao (*Svenson 11024*, 22.3.1941: CAS, GH, NY, UC, US); Guayaquil (*Andersson 76*, 1852: S; *Asplund 15348*, 6.2.1955: S; *Little 6578*, 6.6.1943: F, NY, UC, US); N of Guayaquil (*Fagerlind 166/167*, 13.9.1952: S); Rio Macul (*Fagerlind 32196*, 29.9.1952: S); Guayaquil-Salinas (*Hitchcock 20098*, 21–24.6.1923: GH, US); Samborondon (*Zuber s.n.*, 27.2.1983: ZT); Pedro J. Montero (*Bonifaz & Cornejo 3901*, 9.1.1999: GUAY); Loma Alta (*Cornejo & Bonifaz 6349*, 14.6.1998: GUAY); Milagro (*Cornejo & Bonifaz 6826*, 21.3.1999: GUAY); Isla Puná, Campo Alegre – Agua Piedra (*Madsen 63608*, 7.6.1987: AAU, ZT); Isla Puná, Puná Vieja (*Madsen 63302*, 7–8.5.1987: AAU, ZT); Isla Puná, Concordia (*Madsen 64044*, 9.10.1987: AAU, ZT). Prov. Manabí, 5 km E of Chone (*Bravo 41*, 12.8.1980: QCA). Prov. Oro: Portovelo, Zaruma (*Hitchcock 21258*, 1.9.1923: GH, US). Prov. Pastaza, Rio Capihuari, 76° 50–55′W, 2° 30–31′S (*Ollgard et al. 35062*, 23.7.1980: AAU, US)

Lemna valdiviana: Prov. Chimborazo, 5 km N of Huigra (*Camp 3254*, 19.5.1945: S; *Fagerlind 1325*, 18.11.1952: S); vicinity of Huigra (*Hitchcock 20401*, 7.1923: GH, NY, US; *Hitchcock 20393*: S, US). Prov. Guayas, 10 km N of Guayaquil (*Lüönd s.n.*, 20.11.1984: ZT). Prov. Manabí, 5 km E of Chone (*Bravo*, 15.8.1980: QCA). Prov. Zamora-Chinchipe, between Loja and Zamora (*Sparre 18967*, 25.9.1967: S).

Lemna minuta: Prov. Chimborazo, vicinity of Huigra (*Hitchcock 20401*, 7.1923: NY, US; *Rose & Rose 22264*, 21.8.1918: NY); Laguna de Colta (*Terneus et al*., 20.3.1997: QCA); Huataxi (ex. Herb. Reichenbach fil. *s.n.*, 8.1858: STU). Prov. Imbabura, Lago San Pablo (*Fagerlind 1325*, *1325bis*, 18.11.1952: S). Prov. Pichincha, Machachi (*Holmgren 947*, 13.11.1920: S, ZT); Tandapi (*Maas & Bery et al*. *2894*, 11.9.1977: U); Quebrada del Rio Chiche (*Terneus & Terneus s.n.*, 15.7.1997: QCA).

Wolffiella welwitschii: Prov. Guayas, Guayaquil-Salinas (*Hitchcock 20098*, 21–24.6.1923: GH, US); Milagro (*Hitchcock 20251*, 2.7.1923: US). Prov. Manabí, 5 km E of Chone (*Bravo 41*, 12.8.1980: QCA).

Wolffiella lingulata: Prov. Guayas, 10 km N of Guayaquil (*Lüönd s.n.*, 20.11.1984: ZT).

Wolffiella oblonga: Prov. Imbabura, Lago San Pablo (*Camp 3254*, 19.5.1945: S; *Fagerlind 1325bis*, 18.11.1952: S). Prov. Chimborazo, Laguna de Colta (*Terneus et al*. *s.n.*, 20.3.1997: QCA).

Wolffia brasiliensis: Prov. Guayas, N of Guayaquil (*Fagerlind 166/167*, 13.9.1967: S).

Wolffia columbiana: Prov. Esmeraldas, 25 km S of Esmeraldas (*Sparre 15451/52*, 12.4.1967: S). Prov. Guayas, Guayaquil (*Andersson 67*, 1852: S; *Asplund 15348/49*, 6.2.1955: S; *Little 6578*, 6.6.1943: NY); N of Guayaquil (*Fagerlind 166/167*, 13.9.1952: S).

Vegetation studies

If we compare the present relevés (Tables 3–8) with the vegetation survey in Landolt (1999), we recognize that most of them (Tables 3–7) correspond to the units described there, though sometimes with characteristic differences.

The relevés of Table 3 can be attributed to the *Azollo filiculoides-Lemnion gibbae*, an alliance which is distributed in California, higher parts of Mexico, in the southern part of South America and in the Andes. The first three columns belong to the association *Lemno minutae-Lemnetum gibbae* Libermann Cruz *et al*. 1988, the others to the *Azollo filiculoides-Wolffielletum oblongae* Landolt 1999. The first association is more pioneer vegetation or grows in the coolest places, the second one, especially if it contains *Wolffiella*, is characteristic for more stable conditions and does not survive in periodically frozen

Table 3. *Azollo filiculoides-Lemnion gibbae* Landolt 1999. Relevés with cover abundance values according to Braun-Blanquet from + to 5. The localities of relevés are described in Table 1. SF1: species frequencies the Ecuadorian relevés. SF2: Species frequencies calculated on the basis of 59 other South American relevés (Landolt 1999). C: water conductivity in µS cm^{-1}; pH: pH of the water measured in the field.

Species	No. of relevé									SF1	SF2
	6	7	9	8	1	3	2	4	5		
Azolla filiculoides	+	5	2	5	5	1	4	2	1	V	V
Lemna gibba		+	5	1	1	1	3			IV	V
Lemna minuta	3	1	1			+	3			III	IV
Lemna valdiviana			3	3	+	+				III	III
Wolffia brasiliensis					2	2	+	+	+	III	II
Spirodela intermedia					+	+				II	I
Wolffiella oblonga				4						I	III
Wolffia columbiana										0	III
Ricciocarpus natans										0	II
Limnobium laevigatum										0	II
Ceratophyllum demersum										0	I
Salvinia herzogii										0	I
Wolffiella lingulata										0	I
Azolla caroliniana										0	I
Salvinia minima										0	I
Utricularia gibba										0	I
Pistia stratiotes										0	I
C	280	920	550	690	230	–	450	440	450		
pH	7.8	8.5	7.4	7.5	9.2	–	7.1	8.4	8.4		

waters. A comparison of the species frequency of the alliance in Ecuador and in other parts of South America shows not much difference, except that a few species are missing in the Andes of Ecuador (e.g. *Wolffiella lingulata*, *Salvinia* sp., *Limnobium levigatum*). These species have their distribution centre in warmer regions and grow only in transitional vegetation.

Tables 4 to 6 contain relevés of the alliance *Salvinio minimae-Lemnion aequinoctialis* Landolt 1999. Compared to relevés from other parts of South America (Landolt 1999), *Salvinia* is rather rare in Ecuador. On the other hand, *Spirodela polyrrhiza* is wide-spread and gives reason to form geographical variants within the corresponding units. The *Lemno aequinoctialis-Wolffielletum lingulatae* Landolt 1999 (Table 4) and the *Lemno aequinoctialis-Wolffielletum welwitschii* Landolt 1999 (Table 5) are otherwise quite similar in the different geographical regions. The second association of the alliance (*Salvinio minimae-Lemnion aequinoctialis* Landolt 1999) is characterized by the presence of *Wolffiella welwitschii* and by a lower presence of *Azolla caroliniana* and *Lemna valdiviana* than the first association. Table 6 shows some relevés which cannot be attributed to one or the other of the two associations, because they are only fragmentary and lack the typical second layer of more stable and developed assemblages with *Wolffiella* sp. and *Lemna valdiviana*.

Table 4. *Lemno aequinoctialis-Wolffielletum lingulatae* Landolt 1999. Relevés with cover abundance values according to Braun-Blanquet from + to 5. The localities of relevés are described in Table 1. SF1: species frequencies from the Ecuadorian relevés; SF2: species frequencies calculated on the basis of 63 other South American relevés (Landolt 1999); C: water conductivity in µS cm^{-1}; pH: pH of the water measured in the field.

Species	No. of relevé											SF1	SF2
	46	22	61	47	26	45	60	56	19	57	69		
Wolffiella lingulata	2	+	3	1	2	1	4	1	2	+	3	V	V
Lemna aequinoctialis	1	5	1	1	3	3	1	2				IV	V
Lemna valdiviana	2	+	+	1					2	2	3	IV	IV
Azolla caroliniana	1	+			1				1			III	IV
Salvinia minima	2		+	+				1			2	III	III
Pistia stratiotes			+				+	+	+		+	III	III
Wolffiella oblonga			2	4								II	III
Ricciocarpus natans								1		4		II	III
Wolffia columbiana			+	2	1						1	III	II
Spirodela intermedia	3								3			II	II
Limnobium laevigatum				2						1		II	II
Spirodela polyrrhiza	+	+	1	2	1	4	+	1			+	V	I
Wolffiella welwitschii	1		1		1							II	I
Landoltia punctata				+		1						II	0
Wolffia globosa					1							I	0
Ceratophyllum demersum			+									I	0
Lemna obscura							1					I	0
Wolffia brasiliensis												0	II
Utricularia gibba												0	II
Salvinia martyi												0	II
Ceratophyllum echinatum												0	I
Ceratopteris pteridioides												0	I
C	1150	2320	690	1000	970	770	450	720	50	500	520		
pH	7.3	7.6	7.3	7.0	7.3	7.8	6.8	7.3	6.4	7.9	7.4		

Relevés which belong to the *Wolffio columbianae-Lemnion obscurae* Landolt 1999 are shown in Table 7. However, they can be distinguished from the *Wolffio globosae-Lemnetum obscurae* Landolt 1999 of Colombia by the presence of *Spirodela polyrrhiza* and by the scarce occurrence of *Wolffia columbiana*. The association is named here provisionally *Spirodelo polyrrhizae-Lemnetum obscurae* with *Spirodela polyrrhiza* as the characteristic species. The relevé 63 is typical for this unit. The last successional stage of these assemblages with *Wolffiella lingulata* is rarely achieved. In the southeastern states of the USA the association is replaced by the *Lemno valdivianae-Wolffielletum gladiatae* Landolt 1981 of the same alliance.

Relevés with *Landoltia punctata* (Table 8) are not presented in Landolt (1999). They belong to a new alliance within the order of *Lemnetalia aequinoctialis*. This alliance, which is provisionally named here *Lemnae aequinoctialis-Landoltion punctatae*, is char-

Table 5. *Lemno aequinoctialis-Wolffielletum welwitschii* Landolt 1999. Relevés with cover abundance values according to Braun-Blanquet from + to 5. The localities of relevés are described in Table 1. SF1: species frequencies from the Ecuadorian relevés; SF2: species frequencies calculated on the basis of 24 other South American relevés (Landolt 1999); C: water conductivity in µS cm^{-1}; pH: pH of the water measured in the field.

Species	No. of relevé									SF1	SF2
	52	54	42	48	26	55	46	61	70		
Wolffiella welwitschii	3	3	4	3	1	3	1	1	2	V	V
Wolffiella lingulata			2	1	2	2	2	3	2	IV	III
Lemna aequinoctialis		+		+	3	1	1	1	4	IV	V
Salvinia minima	2	2				2	2	+	2	IV	III
Spirodela polyrrhiza				2	1	+	+	1	3	IV	0
Lemna valdiviana			1	3			2	+	1	III	I
Pistia stratiotes						+		+	+	II	IV
Wolffia columbiana					1			+	1	II	III
Azolla caroliniana					1		1		+	II	I
Wolffiella oblonga						1		2		II	I
Limnobium laevigatum		1				4				II	I
Spirodela intermedia				+			3			II	I
Wolffia globosa					1				1	II	0
Utricularia gibba						1				I	II
Ceratophyllum echinatum									3	I	I
Lemna obscura									1	I	0
Ceratophyllum demersum								+		I	0
Salvinia martyi										0	III
Ceratopteris pteridioides										0	II
C	1700	350	360	740	970	190	1150	690	1230		
pH	7.0	7.5	7.3	7.2	7.3	7.1	7.3	7.3	8.3		

Table 6. Relevés of the *Salvinio minimae-Lemnion aequinoctialis* Landolt 1999 which cannot be classified into lower-rank units. Cover abundance values from + to 5 according to Braun Blanquet. The localities of relevés are described in Table 1. C: conductivity in µS cm^{-1}; pH: pH of the water measured in the field.

Species	No. of relevé										
	23	36	37	66	53	41	67	38	27	28b	71
Lemna aequinoctialis	3	+	3	2	2	2	2	4	1		2
Azolla caroliniana	+	2	+	1	1	+				2	
Spirodela polyrrhiza	3	+	1	3			5	3		4	
Wolffia columbiana			3		1		3	3	1	2	
Wolffia globosa	1				1				1		2
Pistia stratiotes						1	+				1
Salvinia minima						2					1
Wolffia brasiliensis									4	3	
Spirodela intermedia											5
Ceratophyllum demersum									3		
Landoltia punctata			2								
C	1160	74	1010	470	1710	900	840	1260	370	230	500
pH	7.4	6.5	7.7	7.3	8.4	7.5	8.0	7.6	8.4	7.3	7.2

Table 7. *Wolffio columbianae-Lemnion obscurae* Landolt 1999. Relevés with cover abundance values according to Braun-Blanquet from + to 5. The localities of relevés are described in Table 1. SF1: species frequencies from the Ecuadorian relevés; SF2: species frequencies calculated on the basis of 16 other South American relevés (Landolt 1999); C: water conductivity in µS cm^{-1}; pH: pH of the water measured in the field; SF3: species frequencies calculated on the basis of relevés of the Coastal Plain of the Carolinas (USA) (Landolt 1981).

Species	No. of relevé							SF1	SF2	SF3
	68	59	63	64	60	65	70			
Lemna obscura	5	5	5	2	1	1	1	V	V	IV
Spirodela polyrrhiza		+	1	4	+	2	3	V	0	V
Lemna aequinoctialis	1			3	1	3	4	IV	V	II
Wolffia columbiana							1	I	V	II
Wolffia globosa			3			1	1	III	IV	0
Wolffiella lingulata					4		2	II	I	0
Pistia stratiotes			+		1			II	III	0
Azolla caroliniana			+				+	II	II	0
Ceratophyllum echinatum			2				3	II	I	0
Lemna valdiviana							1	I	I	IV
Limnobium laevigatum	2							I	I	0
Wolffiella welwitschii							2	I	I	0
Salvinia minima								0	II	0
Salvinia martyi								0	I	0
Salvinia sprucei								0	I	0
Wolffiella oblonga								0	I	0
Wolffia elongata								0	I	0
Utricularia gibba								0	I	0
Ceratopteris pteridioides								0	I	0
Spirodela intermedia								0	I	0
Wolffia brasiliensis								0	I	IV
Utricularia purpurea								0	0	III
Limnobium spongia								0	0	III
Wolffiella gladiata								0	0	IV
Ceratophyllum demersum								0	0	II
C	1800	5270	670	430	440	310	1230			
pH	7.0	7.5	8.0	7.1	6.8	7.4	8.3			

acterized by *Landoltia punctata* and *Lemna aequinoctialis*. In most parts of the world *Spirodela polyrrhiza* is an important species of the alliance, and in America also *Azolla caroliniana* as well. In America the alliance can be differentiated according to the species of the second layer in well developed assemblages: in Ecuador *Wolffiella lingulata*, in Rio de Janeiro *Wolffiella neotropica* (relevés a–c made by the author in 1983), and in the southeastern states of the USA (relevé d from Landolt 1981) and in Mexico *Wolffiella gladiata*. The provisional name of the present association is proposed as *Wolffielletum lingulatae-Landoltietum punctatae*.

Table 8. *Lemno aequinoctialis-Landoltion punctatae* nom. prov. Relevés with cover abundance values according to Braun-Blanquet from + to 5. The localities of relevés are described in Table 1. The relevés a, b, c, and d originate from Brazil, coastal region north of Rio de Janeiro (Landolt unpubl.); the relevés e and f originate from the coastal region of North Carolina (Landolt 1981). SF: species frequencies calculated on the basis of the Ecuadorian relevés; C: water conductivity in µS cm^{-1}; pH: pH of the water measured in the field.

Species	No. of relevé										SF	a	b	c	d	e	f
	44	37	30	47	45	43	28a	34	20	72							
Landoltia punctata	3	2	3	+	1	5	3	4	5	4	V	2	3	2	+	3	2
Spirodela polyrrhiza	2	1	2	2	4	2	2	1			V					1	+
Lemna aequinoctialis	3	3	2	1	3	+			2		IV	3	2	2		2	2
Azolla caroliniana	2	+	1				2		+	2	IV	4	4	4	3	+	
Wolffiella lingulata	3			1	1				+		III						
Wolffia brasiliensis							4	4		4	II						
Lemna valdiviana				1			3		+		II				4	1	3
Wolffia columbiana		3		2				+			II						
Wolffia globosa		2					1				II						
Salvinia minima			+	+							II						
Wolffella oblonga				4							I						
Limnobium laevigatum				2							I						
Wolffiella neotropica											0			2			
Wolffiella gladiata											0					5	
Spirodela intermedia															2		
Ricciocarpus natans															3		
Salvinia auriculata															1		
C	76	1010	93	1000	770	2480	240	230	200	65							
pH	6.5	7.7	7.6	7.0	7.8	7.6	7.4	6.6	6.7	6.3							

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