THE TAXONOMY OF NAIADES INHABITING A LAKE ENVIRONMENT.

By Henry van der Schalie.

(Read before the Society, 2nd February, 1940.)

As our knowledge concerning the ecology and distribution of certain groups of animals increases it becomes necessary in the light of this information to evaluate some of the nomenclature that has come into general use. Many attempts at classification have resulted in artificial arrangements. Revisions are then needed to correct these to a more natural system. This need is especially paramount in certain groups. With this problem in mind the following considerations are given regarding the taxonomy of lake-inhabiting Naiades.

It has been known for some time that mussels living in a lake * environment often tend to become dwarfed or stunted. As early as 1834, Isaac Lea named Symphynota benedictensis which we now recognize as a lake form of Anodonta grandis. A few years later DeKay (1843) applied the name rosaceus to the stunted lake form of Lampsilis siliquoidea. Both species are common in the small inland lakes of the glaciated portions of the upper Mississippi and St. Lawrence drainages. It is not surprising, therefore, that these lake-forms were early named. On the other hand, the larger lakes such as Chautauqua Lake, New York, Lake Erie, and Lake Winnebago, Wisconsin, which harbour an unusually great number of naiad species, were not carefully investigated till comparatively recent time. Not until the twentieth century did the application of special names to lake forms become a common procedure, and as a result most species displaying lake-inhabiting characteristics were named by present-day conchologists.

Lake Erie, particularly the west end, is remarkable for its rich naiad fauna. No other lake anywhere harbours so many species of mussels. Consequently, this lake is the type locality for several lake-forms. Walker (1898, 1913) has shown that this abundance is directly the result of a post-glacial invasion into Lake Erie of Mississippi mussels when a connection existed between the waters of the St. Lawrence and Mississippi drainages by way of the Maumee River outlet. With a mussel fauna of approximately thirty species and a variety of ecological conditions the western portion of Lake Erie affords good opportunities for studies on the

response of Naiades to different ecological factors.

Brown, Clark, and Gleissner (1938) made commendable use of the facilities available in western Lake Erie to investigate the causes of dwarfing among lake-dwelling mussels. Their st show that the degree of stunting in mussels is with the degree of exposure to which Naiades are normal habitat. It is not necessary to review the on the basis of what is now known concerning. effect of shoal exposure on mussels in lakes, it is a reference be made to the taxonomic implication naming of ecological forms. An examination current taxonomy is desirable for several reason us better to appreciate difficulties when dealing forms; (2) it may give an evaluation of the s significance of some names now in use; and (; matters for those who are not taxonomists but v in proper designations in the use of many name intergrading forms.

Some of the more common environmental: accredited to Lake Erie and other large lakes are

- I. Fusconaia flava parvula Grier. This form w in 1918. That parvula was merely an ecological fo long before Grier named it. Whether or not warrants subspecific status is open to question, light of what is now known of the variation of 1 Lake Erie.
- 2. Quadrula pustulosa prasina (Conrad). Ort. (1922, 16) join schoolcraftensis and prasina. Th recognized by Ortmann (1919) and F. C. Baker found in Lake Erie.
- 3. Quadrula quadrula (Raf.). No form has been actually a form is recognized. Ortmann (1919, 43 says that the Lake Erie form is 'little inflated and h
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er (1938) made commendable use of the Lake Erie to investigate the causes of dwarfing among lake-dwelling mussels. Their studies conclusively show that the degree of stunting in mussels is directly correlated with the degree of exposure to which Naiades are subjected in their normal habitat. It is not necessary to review their work here, but on the basis of what is now known concerning the environmental effect of shoal exposure on mussels in lakes, it is advisable that some reference be made to the taxonomic implications involved in the naming of ecological forms. An examination of the validity of current taxonomy is desirable for several reasons: (1) It enables us better to appreciate difficulties when dealing with intergrading forms; (2) it may give an evaluation of the significance or insignificance of some names now in use; and (3) it may simplify matters for those who are not taxonomists but who are interested in proper designations in the use of many names now applied to intergrading forms.

Some of the more common environmental forms of Naiades accredited to Lake Erie and other large lakes are as follows:—

- 1. Fusconaia flava parvula Grier. This form was named by Grier in 1918. That parvula was merely an ecological form was recognized long before Grier named it. Whether or not its configuration warrants subspecific status is open to question, particularly in the light of what is now known of the variation of this species within Lake Erie.
- 2. Quadrula pustulosa prasina (Conrad). Ortmann and Walker (1922, 16) join schoolcraftensis and prasina. The prasina form is recognized by Ortmann (1919) and F. C. Baker (1928) as the form found in Lake Erie.
- 3. Quadrula quadrula (Raf.). No form has been named, although actually a form is recognized. Ortmann (1919, 43) wrote: "Sterki says that the Lake Erie form is 'little inflated and has few tubercles'."
- 4. Amblema costata plicata (Say). Ortmann and Walker (1922, 13) gave specific rank to this form. F. C. Baker (1928, 79–80) admits that plicata is a lake form but suggests that it should be written as though it were a distinct species.
- 5. Cyclonaias tuberculata (Raf.). A special form name has not been applied to specimens from Lake Erie, although actually there are specimens available which show a high degree of stunting. To be consistent a special name should apply here as well.
- 6. Pleurobema cordatum pauperculum (Simpson). This is the same as variety magnalacustris of Simpson (1914, 884). Ortmann (1919, 84) states: "I have not seen any specimens grading toward the parent-form, and for this reason we might perhaps be justified in regarding this as a true species." However, Ortmann clearly did not wish to make the necessary change because of a lack of sufficient

material. From what we now know concerning the variation of other species of Naiades in Lake Erie there is every reason to believe that intergrading specimens do exist.

7. Elliptio dilatatus sterkii Grier. Although Grier described this as a distinct variety Brown, Clark, and Gleissner (1938, 689) have shown that: "According to height, all of our specimens (those from the river as well as the lake) belong to the stream variety while according to obesity they would all become sterkii. We seriously doubt the validity of varieties based upon such characters."

8. Anodonta grandis footiana (Lea). Certain conditions in lakes give rise to the footiana form of grandis. Although Ortmann (1919, 148) was inclined to consider footiana as a geographical race of grandis, he indicated that both footiana and benedictensis were "distinctly dependent on ecological conditions", and that they were connected by intergrades. Recent studies reveal that similar conditions anywhere will produce similar forms among Naiades so that the concept of geographical races in the grandis group is untenable.

9. Anodonta imbecillis fusca F. C. Baker. This dwarfed form of imbecillis according to Baker represents an ecological variety, and is reported by him from the open shore of Sturgeon Bay, Wisconsin. He (1927, 222) writes: "It appears to be a dwarfed form of imbecillis produced, probably, by its habitat in a turbulent bay..." Similar forms appear under similar circumstances in western Lake Erie and elsewhere.

is an ecological form is clearly indicated by Ortmann (1919, 170–171) in his discussion of this form in Lake Erie. Of considerable interest in this connection is a supposed new species of Anodontoides named birgei by F. C. Baker (1923, 123). Baker (1928, 182) states that birgei is a form produced by a lake environment and adds: "It is possible that the buchanensis listed by Ortmann as living in Lake Erie may readily be a form of birgei." This procedure of naming ecological forms and even elevating them to the rank of good species is quite illustrative of the dangers which attend a taxonomy that fails to take into account intergrading forms.

rhombicus is not generally applied to the Lake Erie form, F. C. Baker (1922, 132) states that Anthony's rhombica "appears to fit this form and renders a new name unnecessary". The variation of this species has been discussed by van der Schalie (1938, 58) and it is suggested that the range of variation in rugosus is so great that it is not expedient to refer extremes of variation to subspecific categories which have been artificially erected.

of naming the lake form of this species l Schalie, 1938, 58-59). As in the case becomes impracticable to apply name even though it is of interest to obser correlated with the environment.

13. Lasmigona costata eriganensis Gric named as a distinct variety by Grier (subspecies is doubtful because it will to recognize this variety as it is to ac and Fusconaia flava parvula, which we

14. Lasmigona complanata katherin complanata have not been found in Lak from Lake Huron by Goodrich and However, this species has been repo (van der Schalie, 1938, 54–55) making lake form, katherinae, may occur in form is produced in exposed conditionight well be considered with other:

15. Ptychobranchus fasciolaris lacustr known that a stunted lake form of this Ortmann (1919, 210) did not think "i lake-form by a varietal name, but the race is clearly indicated in this case' (1928a, 52) suggested that a special n Brown, Clark, and Gleissner (1938, variation of fasciolaris in Lake Erie, that varieties named on the basis of significance in this species."

16. Obliquaria reflexa Rafinesque. 2 stated: "There is a dwarf race in La possibly deserves a varietal name," special name to this form.

17. Proptera alata (Say). Since L this species, a form name cannot be a form. Ortmann (1919, 255) called a suggested that the form from rivers alata megaptera, if a nomenclatorial of this species is to be made. T Brown, Clark, and Gleissner (1938), Erie, clearly shows that it is not fe forms.

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y erected.

12. Alasmidonta calceolus magnalacustris F. C. Baker. The matter of naming the lake form of this species has been discussed (van der Schalie, 1938, 58-59). As in the case of other ecological forms it becomes impracticable to apply names to extremes of variation, even though it is of interest to observe that such variations are correlated with the environment.

13. Lasmigona costata eriganensis Grier. This ecological form was named as a distinct variety by Grier (1918, 10). Its validity as a subspecies is doubtful because it will most likely prove as unwise to recognize this variety as it is to accept Elliptio dilatatus sterkii and Fusconaia flava parvula, which were named simultaneously.

Specimens of 14. Lasmigona complanata katherinae (Lea). complanata have not been found in Lake Erie, but they are reported from Lake Huron by Goodrich and van der Schalie (1932, 9). However, this species has been reported from the Huron River (van der Schalie, 1938, 54-55) making it highly probable that the lake form, katherinae, may occur in Lake Erie. Obviously this form is produced in exposed conditions of lake environment and might well be considered with other forms similarly produced.

15. Ptychobranchus fasciolaris lacustris F. C. Baker. It is generally known that a stunted lake form of this species occurs in Lake Erie. Ortmann (1919, 210) did not think " it advisable to distinguish the lake-form by a varietal name, but the tendency to develop a local race is clearly indicated in this case". Nevertheless, F. C. Baker (1928a, 52) suggested that a special name should be applied. But Brown, Clark, and Gleissner (1938, 690), in their study of the variation of fasciolaris in Lake Erie, conclude: "It seems to us that varieties named on the basis of size variation alone have no significance in this species."

16. Obliquaria reflexa Rafinesque. Although Ortmann (1919, 215) stated: "There is a dwarf race in Lake Erie, light in colour, which possibly deserves a varietal name," no one has as yet applied a

special name to this form.

17. Proptera alata (Say). Since Lake Erie is the type locality of this species, a form name cannot be applied to distinguish the lakeform. Ortmann (1919, 255) called attention to this condition, and suggested that the form from rivers should be known as Proptera alata megaptera, if a nomenclatorial distinction between the forms of this species is to be made. The variation demonstrated by Brown, Clark, and Gleissner (1938), in their study of alata in Lake Erie, clearly shows that it is not feasible to name these ecological forms.

18. Leptodea fragilis lacustris F. C. Baker. The marked variation of fragilis in Lake Erie is strikingly shown by Brown, Clark, and Gleissner (1938, 693). Ortmann (1919, 249) also recognized this fact and consequently did not feel that a name should be applied to the extremes of variation within fragilis.

19. Obovaria leibii (Lea). It has long been known that leibii is merely the lake form of O. subrotunda. Ortmann (1919, 225) clearly stated this: "Another 'species' distinguished by Lea (and Simpson), O. leibii, is nothing but the form from Lake Erie of O. subrotunda."

20. Ligumia nasuta (Say). Ortmann (1919, 275) states: "There is not much variability in E. nasuta." However, Brown, Clark, and Gleissner (1938, 694) have shown that this species becomes definitely stunted much as other species of mussels do upon exposure. In the Huron River (a tributary of Lake Erie) two specimens were reported as river-mouth inhabitants by van der Schalie (1938, 64). Their size indicates that this species reacts to river conditions in a way similar to Ligumia recta latissima, the river form of Ligumia recta. The following measurements are given to indicate the comparatively large size of the two river-inhabiting nasuta taken from the mouth of the Huron River in Michigan :-

Number of Specimens.				Diameter in mm.	Obesity.	Locality.
ı	13	115	44			Huron River, Flat Rock.
I	12	114	48	36.2	.320	Huron River, E. of Willow.

None of the specimens reported by Ortmann (1919) or by Brown and others (1938) are as large as those reported here.

- 21. Ligumia recta (Lamarck). Since the stunted lake-form recta was originally described from Lake Erie, as pointed out by Ortmann (1919, 279), the name recta is retained for the lake form. L. recta latissima is then generally applied to the form inhabiting rivers. Brown, Clark, and Gleissner (1938, 695) state: "Grier (1920) gives the Lake Erie form the varietal name of latissima but fails to show as great a difference between the lake and stream form as we found within the lake itself."
- 22. Micromya iris novi-eboraci (Lea). This variety is considered to be (Ortmann, 1919, 270) the form common to Lake Erie. However, the distinction is made on the basis of colour pattern, which in specimens from the Huron River (van der Schalie, 1938, 63) was found to be an unreliable criterion in the separation of iris and novi-eboraci. As for size, iris becomes stunted in a lake environment but this has never been emphasized by the application of a special name.

23. Lampsilis siliquoidea rosacea evidence indicating a marked respor ment is found among specimens o 291), van der Schalie (1938, 68-9) complete intergradation between and normal siliquoidea. However, (1938, 697) in comparing size diffe "It is doubtful whether these diff nomically, since the variation within the difference between lake and str considerable doubt on the validity and chadwicki described by F. C. B

24. Lampsilis ventricosa canaden canadensis to ventricosa is much ! siliquoidea. Brown, Clark, and Gl a direct correlation between the de of exposure within portions of we taken into account there is little I as lurida Simpson (1914, 41), peri or winnebagoensis F. C. Baker (19:

25. Truncilla truncata lacustris truncata from Lake Erie are defini 228) suggests that these forms n The variation of truncata within L it unreasonable to apply special na

26. Truncilla donaciformis (Lea) Erie is usually smaller than trunca ably stunted in a lake environme F. C. Baker named a lake form c special name for the lake form o 231) states: "The same relative also occurs in donaciformis." Th that those who would advocate themselves too convinced that it i

27. Dysnomia triquetra (Raf.). found in Lake Erie. There is som considered the name triangularis later the use of triangularis was c of triquetra in lakes may account name to the dwarfed lake form.

28. Dysnomia perplexa rangian regarding the taxonomic status of rangiana belongs with one or the ance here. In either case rangian CY, VOL. 21, NO. 8, JANUARY, 1941.

mann (1919, 249) also recognized this not feel that a name should be applied within fragilis.

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Height Diameter

in mm.	in mm.	Obesity.	Locality,	
44	36.5	.317	Huron	River,
48	36-5	.320	Huron	Rock. River, Willow

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H. VAN DER SCHALIE: THE TAXONOMY OF NAIADES.

23. Lampsilis siliquoidea rosacea (DeKay). Some of the best evidence indicating a marked response of mussels to their environment is found among specimens of siliquoidea. Ortmann (1919, 291), van der Schalie (1938, 68-9) and others have stressed the complete intergradation between the stunted lake-form, rosacea and normal siliquoidea. However, Brown, Clark, and Gleissner (1938, 697) in comparing size differences conclusively show that: "It is doubtful whether these differences have significance taxonomically, since the variation within Lake Erie itself is greater than the difference between lake and stream forms." These results cast considerable doubt on the validity of such subspecies as pepinensis and chadwicki described by F. C. Baker (1927, 223, and 1928, 279).

24. Lampsilis ventricosa canadensis (Lea). The relationship of canadensis to ventricosa is much the same as that of rosacea to siliquoidea. Brown, Clark, and Gleissner (1938, 699) have shown a direct correlation between the degree of stunting and the amount of exposure within portions of western Lake Erie. When this is taken into account there is little reason for accepting such names as lurida Simpson (1914, 41), perglobosa F. C. Baker (1928, 285), or winnebagoensis F. C. Baker (1928, 291).

25. Truncilla truncata lacustris F. C. Baker. Specimens of truncata from Lake Erie are definitely stunted. F. C. Baker (1928, 228) suggests that these forms may also be referred to lacustris. The variation of truncata within Lake Erie is large enough to make it unreasonable to apply special names to the lake forms.

26. Truncilla donaciformis (Lea). Although donaciformis in Lake Erie is usually smaller than truncata, it also tends to become noticeably stunted in a lake environment. It is indeed surprising that F. C. Baker named a lake form of truncata but failed to suggest a special name for the lake form of donaciformis. Yet Baker (1928, 231) states: "The same relative variation recorded under truncata also occurs in donaciformis." This is inconsistent, or is it possible that those who would advocate naming ecological forms are not themselves too convinced that it is wise to do so?

27. Dysnomia triquetra (Raf.). Stunted forms of triquetra are found in Lake Erie. There is some indication that Walker (1913, 21) considered the name triangularis as applicable to this form. But later the use of triangularis was discontinued. The relative scarcity of triquetra in lakes may account for the failure to apply a special name to the dwarfed lake form.

28. Dysnomia perplexa rangiana (Lea). Considerable doubt exists regarding the taxonomic status of perplexa and torulosa, but whether rangiana belongs with one or the other is not of immediate importance here. In either case rangiana represents the dwarfed lake form

and it shows much the same response to exposure as has been observed in other Naiades.

A Summary of the Environmental Forms of Naiades Inhabiting Larger Lakes in U.S.A.

Name.	Type Locality.	Date.
r. Fusconaia flava parvula Grier.	Lake Erie	1918
2. Quadrula pustulosa prasina (Conrad)	Fox River, at Green Bay	1834
3. Quadrula quadrula (Rafinesque)	Ohio River	1820
4. Amblema costata plicata (Say).	Lake Erie	1817
5. Cyclonaias tuberculata (Rafinesque)	Ohio River	1820
6. Pleurobema cordatum pauperculum		
(Simp.)	Niagara Falls	1900
7. Elliptio dilatatus sterkii Grier	Lake Erie	1918
8 Anodonta grandis tootiana (Lea) .	Lake Winnebago	1840
9. Anodonta imbecillis fusca F. C. Baker	Sturgeon Bay, Wisc.	1927
10. Anodontoides fer. buchanensis (Lea).	Buck Creek, Ohio	1838
11. Strophitus rugosus rhombicus		-06-
(Anthony)	Michigan	1865
12. Alasmidonta calceolus magnalacustris	C. Was Wine	1928
(F. C. Raker)	Sturgeon Bay, Wisc.	1928
13. Lasmigona costata eriganensis Grier.	Lake Erie	1910
14. Lasmigona complanata katherinae	Lake Superior (erroneous)	r838
(Lea) · · · ·	Pake 20 berrot (stroneous)	1030
15. Ptychobranchus fasciolaris lacustris	Chautauqua Lake, N.Y.	1928
F. C. Baker	Kentucky River	1820
16. Obliquaria reflexa Rafinesque	Lake Erie	1817
17. Proptera alata (Say)	Lake Butte des Morts .	1022
18. Leptodea fragilis lacustris (F.C.Baker)	Erie County, Michigan .	
10. Obovaria teion (Lea) · · ·	Delaware and Schuylkill	
20. Ligumia nasuta (Say)	Rivers · ·	1817
* (T amanaly)	Lake Erie	1819
21. Ligumia recta (Lamarck)	Oak Orchard Creek, N.Y.	. 1838
22. Micromya iris novi-eboraci (Lea)	Seneca Lake, N.Y.	1843
23. Lampsilis siliquoidea rosacea (DeKay)	St. Lawrence River	1857
24. Lampsilis ventricosa canadensis (Lea) 25. Truncilla truncata lacustris F. C.	57, 24,17	
	Lake Winnebago	1928
Baker 26. Truncilla donaciformis (Lea)	Ohio	1828
27. Dysnomia triquetra (Rafinesque)	Falls of the Ohio	1820
28. Dysnomia perplexa rangiana (Lea)	Ohio River	1839
20. Dysnomia perpiesa rangiana (Dea)		

In the preceding discussion an effort has been made to show that most mussels inhabiting a lake environment develop stunted forms to which varietal names have usually been applied. If dwarfing were restricted to Lake Erie there would perhaps be occasion to designate the stunted forms as geographic races. But the studies of Brown, Clark, and Gleissner, Ortmann, Grier, F. C. Baker, van der Schalie and others, covering many lakes and streams, reveal that similar ecological forms are produced by similar ecological conditions. It is obvious that unless some endeavour is made to indicate definitely the difference between ecological forms and subspecies an undue amount of confusion will persist in our

taxonomy. If for any reason who a form it would be more sensible siliquoidea form rosacea. A rule misleading emphasis which is place as a subspecific or even as a spec

Other experiments and studies effect of ecological factors on muss aid the taxonomist. Such studies A few attempts have been made in were not successful. Although the that dwarfing among Naiades is experimental evidence is desirable.

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	Type Locality.	Date.
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	Niagara Falls	1900
.	Lake Erie	1918
ea) .	Lake Winnebago	1840
Baker	Sturgeon Bay, Wisc	1927
(Lea).	Buck Creek, Ohio	1838
, ,	•	J.
	Michigan	1865
lacustris	3	
	Sturgeon Bay, Wisc	1928
Grier .	Lake Erie	rģr8
therinae		,
	Lake Superior (erroneous)	1838
lacustris	• • • • • • • • • • • • • • • • • • • •	
	Chautauqua Lake, N.Y.	1928
	Kentucky River	1820
	Lake Erie	1817
.Baker)	Lake Butte des Morts .	1922
	Erie County, Michigan .	1862
	Delaware and Schuylkill	
	Rivers	1817
	Lake Erie	1819
æа) .	Oak Orchard Creek, N.Y.	1838
DeKay)	Seneca Lake, N.Y.	1843
is (Lea)	St. Lawrence River	1857
F. C.		
	Lake Winnebago	1928
	Ohio	1828
1e) .	Falls of the Ohio	1820
Lea) .	Ohio River	1839

an effort has been made to show that e environment develop stunted forms e usually been applied. If dwarfing there would perhaps be occasion to as geographic races. But the studies sner, Ortmann, Grier, F. C. Baker, vering many lakes and streams, reveal 3 are produced by similar ecological it unless some endeavour is made to ence between ecological forms and t of confusion will persist in our

taxonomy. If for any reason whatsoever one wishes to designate a form it would be more sensible to do so as follows: Lampsilis siliquoidea form rosacea. A rule of this sort would eliminate the misleading emphasis which is placed on forms when they are written as a subspecific or even as a specific name.

Other experiments and studies along the lines of testing the effect of ecological factors on mussel characteristics will undoubtedly aid the taxonomist. Such studies as these should be encouraged. A few attempts have been made in mussel transplantation, but these were not successful. Although the evidence at hand would indicate that dwarfing among Naiades is entirely phenotypic, recourse to experimental evidence is desirable to prove that it is not genotypic.

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