

# Systematic and Geographical Notes on *Clausiliidae*.\*)

By

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In a presidential address the Rev. A. H. Cooke has presented to the Malacological Society of London an admirable and clear study of this widely distributed family of land shells<sup>1)</sup>, including a review of the geographical distribution of species and a most valuable comprehensive account showing how far classification based on the structure of the shell alone was able to increase our knowledge of this group. The landshells composing it have always been a most attractive object of study to systematists. Especially the peculiarly adapted clausal apparatus of the shell has been a promising field for research. Even more than in most of the other families of landshells the clausal apparatus of the shell of the *Clausiliidae* had been used as a leading feature, apparently well adapted to serve as a definite characteristic for classification. Not only the different species could thus be distinguished, but the characteristics made out were also used for a subdivision into well defined sections of the genus *Clausilia* itself. In this way the system of *Clausiliidae* became a well founded building. Küster, A. Schmidt, v. Vest and O. Boettger were the most experienced workers on this subject.

\*) This paper was completed early in 1923, but, on the advice of the editor of the Proceedings of the Malacological Society of London was kept back to avoid repetition, as two other papers on a somewhat similar subject were about to appear (A. S. Kennard and B. B. Woodward: Note on the Nomenclature and Systematic Arrangement of the *Clausiliidae*. Proceedings of the Malacological Society of London. Vol. XV. London 1923. page 298—308. — W. A. Lindholm: Revised Systematic List of the *Clausiliidae*. Proceedings of the Malacological Society of London. Vol. XVI. London 1924. page 53—80). Both of them treat the systematic arrangement of A. J. Wagner, give a number of corrections and additions, especially as to the further subdivisions of the subgenera, and correct many of the nomenclatorial errors of this author. Their subject does, however, not compete with the one of this paper which, therefore, is now presented for publication. Originally intended for publication in England, these notes were drawn up in English, and are now published as they were.

1) A. H. Cooke: The genus *Clausilia*: a study of its geographical distribution, with a few notes on the habits and general economy of certain species and groups. Proceedings of the Malacological Society of London. Vol. XI. London 1915. page. 249—269.

In spite of a vast, rich literature on the shells of *Clausiliidae*, the amount of work done on the anatomy of this family has remained comparatively scanty<sup>2)</sup>, and the results of these investigations have been made use of even more rarely for systematic purposes. The first attempt in this direction was made by A. Schmidt in 1855, who placed the species he had examined anatomically into two groups<sup>3)</sup>. Then, based on several own earlier investigations<sup>4)</sup>, follows the first system of this family based on anatomical characters in 1893, that of F. Wiegmann<sup>5)</sup>. Later A. J. Wagner cleared up the anatomical structure of *Clausiliidae* in a series of splendid investigations and, eventually, in 1913, published a system of *Clausiliidae*, which contained a number of new facts, and which subsequently was worked out more elaborately by him<sup>6)</sup>. As Wagner himself says, this system is far from final at present, and, considering the great material still awaiting examination, wants further consolidation. I am not disposed to follow Wagner in every detail, and this is especially true as regards nomenclatorial questions which Wagner treats with a regrettable neglect of earlier authors. Almost contemporaneously with Wagner's principal paper, C. M. Steenberg, in 1914, has published a most excellent study on the anatomical characters of the species of *Clausiliidae* occurring in Denmark<sup>7)</sup>. Finally Z. Frankenberger, in 1916, has

<sup>2)</sup> A list of publications on this object is given in the publication of C. M. Steenberg, referred to in footnote 7.

<sup>3)</sup> A. Schmidt: Der Geschlechtsapparat der Stylommatophoren in taxonomischer Hinsicht gewürdigt. Abhandlungen des Naturwissenschaftlichen Vereines für Sachsen und Thüringen in Halle. 1. Band. 1855—1859. Berlin 1855. pag. 1—52.

<sup>4)</sup> F. Wiegmann: Bemerkungen zur Anatomie der Clausilien. Jahrbücher der Deutschen Malakozologischen Gesellschaft. 5. Jahrgang. Frankfurt a. M. 1878. pag. 157—169. — F. Wiegmann: Anatomische Untersuchung der *Claus. Reiniana* Kob. Jahrbücher der Deutschen Malakozologischen Gesellschaft. 5. Jahrgang. Frankfurt a. M. 1878. pag. 202—207.

<sup>5)</sup> F. Wiegmann: Beiträge zur Anatomie der Landschnecken des Indischen Archipels. In M. Weber: Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien. Band III. Leiden 1893. pag. 112—259. Tab. IX—XVI.

<sup>6)</sup> A. J. Wagner: Die Familie der Clausiliidae. Roßmäublers Iconographie der europäischen Land- und Süßwasser-Mollusken. Neue Folge. 21. Band. Wiesbaden 1913. 22. Band. Wiesbaden 1918. — A. Wagner: Zur Anatomie und Systematik der Clausiliiden. Nachrichtenblatt der Deutschen Malakozologischen Gesellschaft. 51. Jahrgang. Frankfurt a. M. 1919. pag. 49—60, 87—104, 129—147. Archiv für Molluskenkunde. 52. Jahrgang. Frankfurt a. M. 1920. pag. 1—13, 67—78, 97—108, 145—158. — A. Wagner: Die Molluskensammlung des Polnischen Naturhistorischen Staatseuseums in Warschau. I. Neue Gruppen und Formen der Subfamilie Alopiinae. Prace Zoologiczne Polskiego Państwowego Muzeum Przyrodniczego. Annales Zoologici Musei Polonici Historiae Naturalis. Tom I, fasc. 1. Warszawa 1921. pag. 41—56. Tab. I—II.

<sup>7)</sup> C. M. Steenberg: Anatomie des Clausilies Danoises. I. Les Organes Génitaux. Mindeskrift for Japetus Steenstrup. XXIX. Köbenhavn. 1914.

studied the system of *Clausiliidae*<sup>8)</sup>, and in a critique most violent in language, but rather unfounded materially he rides a sharp attack against the solid work of Wagner.

Now, are the results obtained by anatomical investigation in accord with those based on the shell characters alone? It has been shown by Wagner's searching studies that anatomy gives important additional characters for systematic work. Species should best be distinguished, in the future as has been done in the past, by the features of the shell which are most characteristic, the more so as anatomical characters are scarcely variable specifically in a striking manner, and with little deviations are common to whole groups. On the other hand as these anatomical deviations are pronounced in a similar way, they afford an excellent method for the formation of systematic categories of higher rank to embrace series of allied forms. It has been demonstrated that the system based on the shell alone is usually sufficient for the formation of minor subdivisions, and that in these cases it complies with the anatomical structure, but it breaks down, and wants considerable changes, if applied to categories of higher rank. Which is the reason for this? Has there been any mistake in the mode of investigation of the old school? It would appear to me that the reason is the importance of the clausal apparatus of the shell being overestimated by the old school which based their system on the shell alone and easily gave a wrong importance to a striking character of the shell. The value of the clausal apparatus is the main difference of opinion between older and more recent authors. The fact that the general level of organisation does not go parallel with the development of the clausal apparatus of the shell but that quite different groups present analogous stages of development of this structure is the most important result of Wagner's researches. It opens quite new prospects for the classification of *Clausiliidae*.

Wagner's biological statements upon the clausal apparatus of the shell of the *Clausiliidae* are important enough. The great variability of the clausal apparatus already observable, although in a minor degree, in several species as individual variation, appears to be principally produced by climatic factors. This can be most easily observed when mountain living and plain forms are compared with one another. It is a remarkable fact that in many groups mountain forms living in a moist surrounding, have a more simple clausal apparatus than the corresponding forms living in the plain in a dry climate. Thus anatomical examination has proved that groups widely separated from one another by the older school as e. g. *Alopi* H. and A. Ad. and *Herilla* H. and A. Ad. must be united into one genus. Similarly in several other genera, such as e. g. *Delima* Hartm. and *Laciniaria* Hartm., forms with a rudimentary clausal

<sup>8)</sup> Z. Frankenberger: Zur Anatomie und Systematik der Clausilien. Zoologischer Anzeiger. XLVII. Band. Leipzig 1916. pag. 221—236.

apparatus can be found in regions from 1500 to 2000 meters. There are even species (e. g. forms of *Laciniaria* [*Laciniaria*] *biplicata* Mont. and *Laciniaria* [*Laciniaria*] *vetusta* Rossm. from the Balkan Peninsula) where differences in height of 200 to 300 meters result in considerable differences of the clausal apparatus, thus presenting every gradation from the fully developed apparatus of the lowland form to the rudimentary condition found in higher regions in an unbroken series.

Moisture in coast districts appears to have a similar influence upon the development of the clausal apparatus as has a mountain climate. In some species of the genus *Medora* H. and A. Ad. from southern Dalmatia as well as in its subgenus *Albinaria* v. Vest, a remarkably simple clausal apparatus is met with frequently. An equally primitive or even obsolete clausal apparatus is found in the species of the tertiary genus *Triptychia* Sandb., which probably lived in the moist coast climate of the European archipelago of that time.

As a result of his original studies Wagner divides the family *Clausiliidae* into four subfamilies: *Alopiinae*, *Clausiliinae*, *Baleinae*, and *Metabaleinae*, which he defines according to the state of our present knowledge.

Before entering into a discussion of the various subfamilies a nomenclatorial change must be made, as according to priority, the subfamily „*Baleinae*“ of Wagner should be termed *Clausiliinae*, and his „*Clausiliinae*“ *Cochlodininae*. The first who fixed a genotype for the Genus *Clausilia* Drap. 1805 among the species originally included in that genus, was A. Turton who selected *Clausilia bidens* Mont. = *rugosa* Drap. for it<sup>9)</sup>. Therefore, when splitting up the old genus *Clausilia*, this name must remain the genus of *rugosa* Drap. The usual name *Pyrostoma* v. Vest 1867, with *plicatula* Drap. as type, has to fall against *Iphigena* Gray 1821, a name remaining as a subgenus of *Clausilia* Drap. for that group. *Kuzmicia* Brus. 1870 falls into the synonymy of *Clausilia* Drap. sens. strict., which also includes *Erjavecica* Brus. 1870. The genus *Clausilia* sens. strict. of Wagner must be changed into *Cochlodina* Fér. 1821.

The *Cochlodininae*, as would appear from geographical reflections, should contain the main stem of the *Clausiliidae*. It seems probable that this family has been developed in Asia, and that its branches have reached Europe as well as South America and Porto Rico. The main stem is represented by numerous Asiatic *Clausiliidae*, which are split up into a number of genera, formerly as a rule united in the genus *Phaedusa* H. and A. Ad. It remains questionable whether these numerous and, as regards forms, varied species belong to one or more subfamilies; this appears rather doubtful, and must

<sup>9)</sup> A. Turton: Manual of the Land- and Freshwater Shells of the British Islands. 1831. pag. 6.

be shown by a more complete knowledge of their anatomy<sup>10)</sup>. A special group is represented by the Asiatic genus *Garnieria* Bourg., enumerated by Wagner with the *Alopiinae* which are widely distributed in the European faunal region, a classification which appears to me rather improbable; our knowledge of these shells is much too incomplete to allow of a definite opinion as to their systematic position. I am rather inclined to erect for their reception a new subfamily *Garnieriinae*, which might be derived from the *Cochlodininae*. There is also a possibility that the *Garnieriinae*, and not the *Cochlodininae*, are more primitive, a question which can only be decided by anatomical examination of their soft parts. If this should prove to be the case, an old subfamily of the *Clausiliidae* would have been preserved in Asia, while only the more advanced *Cochlodininae* would have developed the present wide distribution of the family. As far as can be judged, however, from the shell, the *Cochlodininae* are the more primitive of the two subfamilies. As regards their shells the *Garnieriinae* come nearest to the American *Clausiliidae* of which the genus *Peruina* Poliński 1921 approaches them most closely in the shape of the last whorl and the aperture. In spite of the great multiplicity in shell forms these American *Clausiliidae* appear to be of rather uniform origin and to belong to one subfamily *Neniinae*. Perhaps the *Neniinae* are derived from the Asiatic *Garnieriinae*, or else both have been developed from the primitive roots of the *Cochlodininae*. To day all this is mere speculation, a definite opinion in either direction being only probable based on detailed anatomical researches which are still wanting. Tertiary *Clausiliidae* from Asia which perhaps also could clear up a lot, are not found until now. The only American tertiary shell, which might be of interest in this connection is *Cirrobasis venusta* Conrad<sup>11)</sup> from the Neogen of Pebos, Upper Marañon, Peru, South America; it is, however, much too insufficiently described and figured to form an opinion upon its systematic position, although it appears to belong to the *Neniinae*.

There are probably no affinities between the South American *Neniinae* and the European genus *Laminiſera* O. Bttg., a view advo-

<sup>10)</sup> The nomenclature of the division of these *Clausiliidae* by A. J. Wagner (loc. cit. 1920, pag. 9—13) cannot be maintained. This author has given no types of his new groups. This was afterwards corrected by A. S. Kennard and B. B. Woodward (Note on the Nomenclature and Systematic Arrangement of the Clausiliidae. Proceedings of the Malacological Society of London. Vol. XV London 1923. pag. 298—308. On pag. 302, 305). Thus *Aprosphyra* Wagn. 1920 is a synonym of *Megalophaedusa* O. Bttg. 1877, and *Macrenoica* Wagn. 1920 to *Pseudonenia* O. Bttg. 1877. *Polyptychoplora* Wagn. 1920 (Type: *elisabethae* v. Möll.) and *Synprosphyra* Wagn. 1920 (Type: *swilla* Bav. et Dautz.) must be maintained.

<sup>11)</sup> T. A. Conrad: Remarks on the clay of the Upper Amazon, with descriptions of new shells. Proceedings of the Academy of Natural Sciences of Philadelphia. Philadelphia 1874. pag. 25—32. On pag. 13; tab. I, fig. 15.

cated especially by J. R. Bourguignat<sup>12)</sup>. The geographical distribution and affinities of the *Clausiliidae* as well as the *Eulotidae* of America point decidedly to the West, towards Asia, not across the Atlantic, towards Europe.

In the European faunal area the *Cochlodininae* are also represented, viz., by the genera *Cochlodina* Fér. 1821, *Charpentieria* Stab. 1864 (= *Dilataria* v. Vest 1867), and *Serrulina* Mouss. 1873; and, in the eastern peripheral districts by one more representative, which has been directly classed with the Asiatic genus *Hemiphaedusa* O. Bttg. 1877 (*perlucens* O. Bttg. from Lenkoran in the Talysh district on the Caspian and from the Tiflis province), if it should not be proved to belong into the vicinity of *Serrulina* Mouss.<sup>12a)</sup>. At present there is undoubtedly no clear connection between the Asiatic and European distributional area of the *Clausiliidae*. According to our present knowledge they appear even to be entirely separated. But there is a probability that a transition will be found along the Iranian mountain chains.

As regards geographical distribution in Europe the *Clausiliidae* differ materially from the *Eulotidae*, which, in their turn, have attained a much wider distribution in America than have the *Clausiliidae*. In Europe the *Eulotidae* belong to the most recent animals and are only represented by the well known species *Eulota* (*Eulota*) *fruticum* Müll. In the European faunal area the *Eulotidae* are replaced by the *Helicidae*, a family autochthonous in this region and undoubtedly closely allied to the *Eulotidae*, from which they have probably been developed by isolation. The *Eulotidae*, have invaded the distributional zone of the *Helicidae* only in most recent geological times. In the *Clausiliidae* a definite separation as in the *Eulotidae* and *Helicidae* has not been affected. It is true that in the European faunal area have been further developed a number of fairly well differentiated forms of *Clausiliidae*, which are best classed as separate subfamilies, while in the more conservative Asia the *Cochlodininae* as well as the *Eulotidae* have in the main kept their old characters. But except the more advanced forms, the *Cochlodininae* survive in Europe in the three indigenous genera *Cochlodina* Fér., *Charpentieria* Stab., and *Serrulina* Mouss., and in the eastern border zone, a doubtful representative of the Asiatic genus *Hemiphaedusa* O. Bttg. During the Tertiary the *Cochlodininae* were still far more dominant in the European faunal area than they are at present, a fact well reconcilable with what has been said above. H. A. Pilsbry has also stated that the East Asiatic *Clausiliidae* are more closely related to early Tertiary than to modern

<sup>12)</sup> J. R. Bourguignat: Histoire des Clausilies de France vivantes et fossiles. Annales des Sciences naturelles de Paris. Paris 1877. Art. No. 10.

<sup>12a)</sup> Recently W. A. Lindholm (loc. cit., pag. 62) has created the new section *Caspiophaedusa* Lindh. for *perlucens* O. Bttg.

European groups.<sup>13)</sup> This is undoubtedly true; for at present the *Cochlodininae* are much less conspicuous in Europe than they were in the early Tertiaries. The earliest fossil representatives of the *Clausiliidae* are known from the Upper Cretaceous. They should undoubtedly be classed with the *Cochlodininae*. They appear to be connected with the European Early Tertiary forms of this family and are probably their ancestors. It is quite likely that even the same genera as in the older Tertiary have existed during the Upper Cretaceous. Thus the species *patula* Math. and *subantiqua* d'Orb. (= *matheroni* Opp.) from the Upper Cretaceous of the Provence should probably be placed into the genus *Neniopsis* Wenz. They are certainly no relations to *Albinaria* v. Vest with which they have been connected by P. Oppenheim.<sup>14)</sup> I am personally not acquainted enough with the Cretaceous *Clausiliidae* to attempt at a final arrangement of the various species into genera. A great variety of forms is attained by the family during Early Tertiary times. I am distinctly inclined to class a number of these genera with the *Cochlodininae*: *Palaeophaedusa* Wenz 1920 (Low. Paleocene), *Neniopsis* Wenz 1920 (Low. Paleocene), *Oospiroides* Wenz 1920 (Low. Paleocene to Middle Eocene), *Euclausta* Oppenh. 1890 (M. Eocene), *Disjunctaria* O. Bttg. 1877 (M. Eocene), *Ptychophaedusa* Wenz 1920 (M. Eocene), *Pachyphaedusa* Wenz 1920 (M. Eocene), ? *Emarginaria* O. Bttg. 1877 (M. Eocene). To conclude an European origin for this family from this early and varied development of forms would certainly be a risk; I should think that these early Tertiary faunas in Europe are merely radiations of an Asiatic fauna specially adapted and transformed in the European coast districts and islands of this period. All of these Early Tertiary European genera disappear in the Middle Eocene; only *Emarginaria* O. Bttg. is an exception, if it is true that the Upper Miocene species *schaefferiana* O. Bttg.<sup>15)</sup> from the brown coal clay of Undorf near Regensburg, Bavaria, upon which the genus *Emarginaria* O. Bttg. was founded, and the Middle Eocene *exsecretata* Oppenh.<sup>16)</sup> from the Roncà strata of Pugniello, Province of Vicenza, Italy, belong to one genus; the hiatus between the two species is certainly remarkable. Also the Lower Oligocene species *physoides* Mill. has

<sup>13)</sup> H. A. Pilsbry: Catalogue of the *Clausiliidae* of the Japanese Empire. Proceedings of The Academy of Natural Sciences of Philadelphia. Vol. LIII. Philadelphia 1901. pag. 647—656.

<sup>14)</sup> P. Oppenheim: Beiträge zur Binnenfauna der provençalischen Kreide. Palaeontographica. Band XLII. pag. 309—378. Taf. XVI—XIX. On pag. 348—350.

<sup>15)</sup> O. Boettger: Clausilienstudien. Palaeontographica. Neue Folge. Supplement. Band III, 1877. pag. 79; tab. III, fig. 28a—f, 29.

<sup>16)</sup> P. Oppenheim: Die Land- und Süßwasserschnecken der Vicentiner Eocänbildungen. Eine palaeontologisch-zoogeographische Studie. Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Klasse. 57. Band. Wien 1890. pag. 113—150. On pag. 129; tab. V, fig. 5—5d.

been regarded as probably belonging to *Neniopsis* Wenz<sup>17)</sup>; this species is only incompletely known from the stony nucleus; but if it should really belong here, the genus *Neniopsis* Wenz would survive from the Middle Eocene to become extinct only in the Lower Oligocene.

The similarity in the shell of these fossil genera of *Clausiliidae* of the European Early Tertiaries with Asiatic *Cochlodininae* is often really striking; the form of the shell in the genus *Oospiroides* Wenz f. i. recalls the Asiatic *Oospira* Blanf. These fossil genera, however, are probably more nearly allied to the European genus *Serrulina* Mouss., which, up to the present, has also kept the peculiar plication of the aperture characteristic of most of the Early Tertiary *Clausiliidae* of Europe. The external form of these Early Tertiary species which is very similar to that of the Asiatic ones would appear to be produced by a warmer climate prevailing in Europe at that time and similar to the present conditions in some different districts of Asia.

The genus *Serrulina* Mouss. appears during the Lower Miocene, but had a much wider distribution in Europe and a greater variety in species than it has now. In fact it survives only in Anterior Asia from the Amanus Mountains across Armenia, Caucasia, and Northern Persia, and as a relict, in caves of the Island of Corfu and Southern Dalmatia (*Serrulina* [*Phygas*] *collasi* Stur.).

Slightly older is *Constricta* O. Bttg. 1877 which should also belong to the *Cochlodininae* and which begins in the Upper Oligocene, but disappears as soon as the Lower Miocene. I should further include in the *Cochlodininae* the genus *Eualopia* O. Bttg. 1877, a genus with a reduced clausal apparatus, which lived in the coast regions of Europe during the Lower Miocene and disappeared later. In the Lower Miocene strata of Bohemia (Landshell limestone of Tuchorschitz) and the Upper Miocene of Styria (Brown coal clay of Rein) the genus *Charpentieria* Stab. 1864, which survives up to the present, is first found. *Cochlodina* Fér. 1821 is only known since the Middle Pliocene (Fresh water marl of Hauterive, Département of Drôme, France).

With the *Cochlodininae* may be connected the tertiary genus *Triptychia* Sandb. 1874<sup>17a)</sup>, which contains a great number of species, and may be subdivided into various subgenera (*Plioptychia* O. Bttg. 1877, *Triptychia* sens. strict. and *Milne-Edwardsia* Bourg. 1877). It is characteristic for the Upper Oligocene to Upper Pliocene coastal districts and insular regions of Europe. As these shells lived in moist coast districts they have been able, by and by, to reduce the clausal apparatus of their shell aperture. This development is progressing from the species older geologically to the more recent ones; the most specialized forms became extinct when the climate changed and readaption probably was impossible.

<sup>17)</sup> W. Wenz: Zur Systematik tertiärer Land- und Süßwassergastropoden. III. Senckenbergiana. Band II, Heft 1. Frankfurt a. M. 1920. pag. 15—18. On pag. 18.

<sup>17a)</sup> I think that *Triptychia* Sandb. 1874 must not be abandoned on account of *Triptycha* Müll. 1859.



Systematically the species of *Triptychia* Sandb. are best regarded as a separate extinct subfamily, *Triptychiinae*, of the *Clausiliidae*; within the *Cochlodininae*, from which they are probably derived, they would appear to be rather isolated.

The next subfamily is restricted to the European faunal area and may have been developed from ancestors allied to the *Cochlodininae*; it has been called *Baleinae* by Wagner, but, as pointed out above, ought to be designated as *Clausiliinae*, as it includes the restricted genus *Clausilia* Drap. Except this genus the following genera belong here: *Neostyria* A. J. Wagn. 1920<sup>18</sup>), *Olympicola* Hesse 1916, *Micropontica* O. Bttg. 1881, *Laciniaria* Hartm. 1842 (with the subgenera *Laciniaria* sens. strict.<sup>19</sup>), *Pseudalinda* O. Bttg. 1877<sup>20</sup>), *Euxina* O. Bttg. 1877, *Mentissa* H. and A. Ad. 1855, and *Euxinastra* O. Bttg. 1888), *Balea* Gray 1824. The separation of this subfamily from Wagner's *Metabaleinae* would appear to me not sharp enough and this subfamily itself not tenable. Wagner himself has already pointed out that they are transitional forms in more than one respect between other main groups of *Clausiliidae*. This is especially true of the genera *Fusulus* Fitz. 1833, and *Graciliaria* E. A. Bielz 1867, which, in the structure of the genital apparatus, recall the restricted genus *Clausilia* Drap. I should therefore unite in the extended subfamily *Clausiliinae* the genera: *Fusulus* Fitz. 1833, *Graciliaria* E. A. Bielz 1867, *Acrotoma* O. Bttg. 1881, *Idyla* H. and A. Ad. 1855 (with the subgenera *Idyla* sens. strict.<sup>21</sup>), and

<sup>18</sup>) *Neostyria* A. J. Wagn. (loc. cit. 1920, pag. 72); synonymous with this name is *Neostyriaca* A. J. Wagn. (loc. cit. 1920, pag. 107).

<sup>19</sup>) According to Wagner's researches (loc. cit. 1920, pag. 105, 106) the groups of *maesta* Fér., *cana* Held, *rugicollis* Rossm., *schwerzenbachi* A. Schm., *plicata* Drap., and *biplicata* Mont. are best united into one subgenus, for which the name *Laciniaria* Hartm. 1842 (J. D. W. Hartmann: Erd- und Süßwasser-Gasteropoden der Schweiz. St. Gallen 1844. pag. 174) is available. This name must also be used for the genus in question. The genus *Balea* Gray 1824 should best be kept separated from *Laciniaria* Hartm. on account of its peculiarities in the clausal apparatus.

<sup>20</sup>) *Uncinaria* v. Vest 1867 and *Pseudalinda* O. Bttg. 1877 should be united into one single subgenus of *Laciniaria* Hartm. As *Uncinaria* v. Vest 1867 is preoccupied by *Uncinaria* Froelich 1789 (Vermes), the subgenus must be designated as *Pseudalinda* O. Bttg. If further sectional names for the different groups of *Pseudalinda* O. Bttg. should be used, the group of *elata* Rossm. must be named as *Vestia* Hesse 1916 (P. Hesse: Kritische Fragmente. Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft. 48. Jahrgang. Frankfurt a. M. 1916. pag. 122—124. On pag. 124).

<sup>21</sup>) The type of *Idyla* H. and A. Ad. 1855 is, according to the fixation of E. von Martens (J. C. Albers: Die Heliceen nach natürlicher Verwandtschaft systematisch geordnet. 2. Ausgabe von E. v. Martens. Leipzig 1860. pag. 284), *bicristata* Rossm. This species has also been chosen by C. A. Westerlund (C. A. Westerlund: Methodus dispositionis Conchyliorum extramarinorum in Regione palaeartica viventium. Rada Jugoslav. Akad. Acta Acad. Sci. Slavorum merid. Vol. 151. Zagrabiae 1902. pag. 111) as type of *Oligoptychia* O. Bttg. 1877; such *Oligoptychia* O. Bttg. 1877 becomes a synonym of *Idyla* H. and A. Ad. 1855, and the genus of *laevicollis* Charp. must be named *Armenica* O. Bttg. 1877. The group of *foveicollis* Charp. (*Scrobifera* O. Bttg. 1877) must be united with *Idyla* H. and A. Ad. 1855 as a subgenus; *Pleioptychia* A. J. Wagn. 1913 is synonymous with it.

*Scrobifera* O. Bttg. 1877), *Armenica* O. Bttg. 1877, *Mentissoidea* O. Bttg. 1877 (= *Polinskia* A. J. Wagn. 1920), and probably also *Laminifera* O. Bttg. 1863, and *Boettgeria* O. Bttg. 1863. It remains doubtful whether a more thorough knowledge of the anatomy of all the genera in question will lead to a further splitting up. As regards the structure of the genital organs the genus *Mentissoidea* O. Bttg. from the Caucasus is the most primitive and most nearly allied to the *Cochlodininae*.

Fossil *Clausiliinae* crop up rather early. If they should have sprung from the *Cochlodininae*, this must have been at rather an early geological epoch; but this is quite possible as the *Cochlodininae* were already present and highly specialized during Lower Paleocene times. The oldest form known of the subfamily *Clausiliinae*, from the Upper Paleocene (Ypresien) „Sables de Cuise“ from the Département Oise, France, which most probably belongs to the still living genus *Laminifera* O. Bttg. is *houdasi* Cossm.<sup>22)</sup>, originally, but most certainly erroneously, described as a member of *Agathylla* H. and A. Ad. The genus *Laminifera* O. Bttg. is widely distributed in the tertiary strata of Europe. Except the typical subgenus, two further fossil subgenera, *Baboria* Cossm. 1892 and *Polloneria* Sacco 1886, should be placed here. There are only two recent species of the typical subgenus *Laminifera* O. Bttg., relicts, living in the Pyrenees; the genus has obviously lost ground.

The genus *Acrotoma* O. Bttg. 1881, at present inhabiting Caucasia and Armenia, according to P. Oppenheim, includes the Middle Eocene species *marcellana* Oppenh.<sup>23)</sup> from the Roncà strata of the Province of Vicenza, Italy. There is a remarkable hiatus in time between the fossil and living shell, and also a wide distance from the present habitat of the genus, a locality, however, rich in archaic species.

A genus well represented in the European Tertiary is *Canalicia* O. Bttg. 1863, which is known with certainty from the Upper Oligocene (*Canalicia articulata* Sandb., from the Land shell limestone of Hochheim and Flörsheim, Hesse-Nassau, Germany). If *densicostulata* Sandb., from the Lower Eocene freshwater limestone of Lower Alsace and Switzerland, is really a *Canalicia*, this genus reaches back to the Eocene. The most recent representative is *Canalicia gonytyx* O. Bttg. from the Marine sands (Vindobonien) of Grund near Vienna, Austria, there are, however, no living forms.

<sup>22)</sup> M. Cossmann: Catalogue Illustré des Coquilles Fossiles de l'Eocène des Environs de Paris. IV Annales de la Société Royale Malacologique de Belgique. Vol. XXIV. Bruxelles 1889. pag. 368; tab. XII, fig. 35—36.

<sup>23)</sup> P. Oppenheim: Die Land- und Süßwasserschnecken der Vincen-tiner Eocänbildungen. Eine palaeontologisch-zoogeographische Studie. Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Classe. 57. Band. Wien 1890. pag. 113—150. On pag. 128; tab. V, fig. 6—6b.

In the Upper Miocene strata of Europe several species of the *Clausiliinae* genus *Pseudidyla* O. Bttg. 1877, are found, which, however, disappear again almost immediately. They appear to be a first wave of new faunal elements from the southeastern European faunal region, which from the Pliocene obtain an increasing influence upon the aspect of the Central European fauna. The genus *Clausilia* Drap. 1805, now so characteristic for the European fauna, is known in the two subgenera *Clausilia* Drap. sens. strict. and *Iphigena* Gray 1821 since the Middle Pliocene. Also the genus *Laciniaria* Hartm. 1842 appears in France at the same time, if the species *fischeri* Mich.<sup>24)</sup>, from the Plaisancien of the Départements of Drôme and Hérault belong here.

In connection with the subfamily *Clausiliinae*, the African representatives of the family may be discussed here. It is not astonishing that *Clausiliidae* occur in North Africa which belongs to the European faunal region; they are, however, not very numerous there. They belong to the *Cochlodininae* and *Alopiinae*. Most of the species are known from Tunesia, and their affinities suggest a connection with Sicily. East and West from Tunesia the number of species decreases, and the family disappears altogether. Another, quite independent, distributional centre of the *Clausiliidae* are the highlands of Abyssinia which are also the home of other European faunal elements. Probably all the Abyssinian *Clausiliidae* described belong to *Macroptychia* O. Bttg. 1877, a genus occurring too in the mountain chains of Yemen (*Macroptychia schweinfurthi* v. Mart.), thus accentuating the near geographical relations existing between the countries east and west of the southern Red Sea. There are some species of *Clausiliidae* extending still further south (*degeneris* Prest. from between Rumruti and Mount Kenya, *giraudi* Bourg. from Pambete on the southern end of Lake Tanganyika). It remains doubtful, whether both belong to *Macroptychia* O. Bttg., although it is probable. This is especially true of *degeneris* Prest.; as regards *giraudi* Bourg., Bourguignat, in addition to characters recalling *Delima* Hartm. finds characters of Asiatic *Cochlodininae*<sup>25)</sup>. This observation is the more remarkable, if the distribution of the *Eulotidae* is born in mind, which originally characteristic for Asia, extends into Central Africa as far as the Congo Basin. The occurrence in Central Africa of *Cochlodininae* with Asiatic affinities is thus also quite possible. On the other hand some European faunal elements which also reach the district of the African Lakes, make it quite possible that those *Clausiliidae* together with the Abyssinian species belong to the European stem of that family.

<sup>24)</sup> A. L. G. Michaud: Description des coquilles fossiles des environs de Hauterive (Drôme). Journal de Conchyliologie. X (Sér. 3, vol. II). Paris 1862. pag. 74; tab. III, fig. 18.

<sup>25)</sup> J. R. Bourguignat: Notice prodromique sur les Mollusques terrestres et fluviatiles recueillis par M. Victor Giraud dans la région méridionale du lac Tanganika. Paris 1885. pag. 22—23.

The anatomy of *Macroptychia* O. Bttg. is unknown. As far as can be judged from the shell, it appears to belong to the *Clausiliinae* which, accordingly, are the most advanced outposts of this family in Africa. Within the subfamily *Clausiliinae*, *Macroptychia* O. Bttg. should range nearest to *Laminifera* O. Bttg. which has also had time enough to extend its territory, but had lost part of it again. The genera *Laminifera* O. Bttg., *Mentissoidea* O. Bttg., *Olympicola* Hesse, *Macroptychia* O. Bttg. and *Boettgeria* O. Bttg. would appear to represent the archaic elements within the subfamily.

A further subfamily of the *Clausiliidae* are the *Alopiinae*. This subfamily includes the following genera: *Papillifera* Hartm. 1842 (with the subgenera *Papillifera* sens. strict., *Isabellaria* v. Vest 1867, and *Leucostigma* A. J. Wagner 1919), *Macedonica* O. Bttg. 1877<sup>26</sup>), *Delima* Hartm. 1842 (with the subgenera *Delima* sens. strict., *Carinigera* v. Möll. 1873, *Siciliaria* v. Vest 1867, and *Lampedusa* O. Bttg. 1877<sup>27</sup>), *Medora* H. and A. Ad. 1855<sup>28</sup>) (with the subgenera *Medora* sens. strict., *Agathylla* H. and A. Ad. 1855, *Albinaria* v. Vest 1867, and *Cristataria* v. Vest 1867), *Triloba* v. Vest 1867, *Protoherilla* A. J. Wagn. 1921, *Alopiia* H. and A. Ad. 1855 (with the subgenera *Herilla* H. and A. Ad. 1855, and *Alopiia* sens. strict.). The *Alopiinae* are characteristic for the European faunal area. Their present centre of distribution is the Balkan Peninsula and the Aegean Islands. From there they have reached Algeria in the West, Syria in the East, and have radiated in a northern direction to the Alps and Carpathians. They have, however, not been able to extend over so wide tracts of country as have the *Cochlodiniinae* and *Clausiliinae*.

Up to now there is no fossil record of the *Alopiinae*. The affinity of certain species from the Upper Cretaceous with *Albinaria* v. Vest, as has been supposed by Oppenheim, appears doubtful. The species in question are, as mentioned above, probably more

<sup>26</sup>) Into this genus *Serbica* O. Bttg. 1877 must be included. The new name *Neoserbica* A. J. Wagn. (A. J. Wagner: loc. cit. 1919, pag. 135—136) is a synonym of *Macedonica* O. Bttg. 1877, as it includes the type of *Macedonica* O. Bttg. as well as the type of *Serbica* O. Bttg. The different making up of the group by Wagner is no reason to do away with existing names.

<sup>27</sup>) Wagner (loc. cit. 1919, pag. 132) took the name of *Mauritanica* O. Bttg. for this subgenus of *Delima* Hartm. If Wagner's composition of this subgenus would be correct, it must be connected with the name of *Lampedusa* O. Bttg. 1877 with the type species *lopedusae* Pfr. (O. Boettger: *Clausilienstudien*. Cassel 1877. pag. 50). *Mauritanica* O. Bttg. 1879 with the type species *tristrami* Pfr. (O. Boettger: *Gattung Clausilia* Drap. *Iconographie der Land- und Süßwasser-Mollusken von E. A. Rossmässler*, fortgesetzt von W. Kobelt. 6. Band. Wiesbaden 1879. pag. 52—158. Taf. 167—178. On pag. 153) as well as *Imitatrix* West. 1884 with the type species *imitatrix* O. Bttg. (C. A. Westerlund: *Fauna der in der paläarktischen Region lebenden Binnenconchylien*. IV Gen. *Balea* Prid. et *Clausilia* Dr. Karlskrona 1884. pag. 57) are synonyms of *Lampedusa* O. Bttg. 1877.

<sup>28</sup>) *Medora* H. and A. Ad. 1855 being older than *Albinaria* v. Vest 1867, it is not admissible to rank the first one as a subgenus of the latter, as Wagner did in his publications.

nearly related to genera of *Cochlodininae* from the Early Tertiaries. Of the Lower Tertiary species *edmondi* Boissy<sup>29)</sup>, *houdasi* Cossm.<sup>30)</sup>, and *bernayi* Cossm.<sup>31)</sup> which Cossmann 1889 has placed into *Agathylla* H. and A. Ad., the last two should go with *Laminiifera* O. Bttg., while for *edmondi* Boissy a special genus, *Palaeophaedusa* Wenz 1920, has been created.<sup>32)</sup>

The *Alopiinae* have probably been developed in the Southeast of the European faunal area, regions which still form their principal habitat, but the Tertiary deposits of which are imperfectly known. I should think, they have sprung therefrom the *Clausiliinae*. The connecting link between them is formed by the genus *Papillifera* Hartm., although the mechanism of the clausal apparatus of the shell belongs to a highly specialized Clausiliid type. But this ought to be of less importance as the clausal apparatus can be adapted to certain climatic conditions. According to Wagner the structure of the sexual organs of *Papillifera* Hartm. is that of the *Alopiinae*, but by the often remarkable thin and long diverticulum of the duct of the seminal vesicle recalls the *Clausiliinae*. In 1913, Wagner still classed *Papillifera* Hartm. with his *Metabaleinae*<sup>33)</sup>, most of which I have placed among the *Clausiliinae*, as has been shown above. Thus, from a geological point of view, the *Alopiinae* appear to be the most recent subfamily of the *Clausiliidae* within the European faunal area and of the *Clausiliidae* in general.

Having discussed the various subfamilies of the *Clausiliidae*, the position of the family itself within the *Stylommatophora* must be regarded. Z. Frankenberger<sup>34)</sup> does not recognise them at all as a family, but regards them as a subfamily of the *Pupillidae*. Wagner<sup>35)</sup>, who treats them as a separate family, unites them with the *Pupillidae* and *Enidae* into one tribe. H. A. Pilsbry's classification, which is founded on the structure of the renal organ and ureter, may or may not be agreed with, the presence of a secondary ureter, in the *Clausiliidae* and its absence in the *Pupillidae* and *Enidae* is much too pronounced a character to be overlooked. The relations of the *Clausiliidae* to these two groups would therefore appear to be not so very close, and I should look for affinities to other groups of the *Sigmurethra*, which, in the structure of their shell, present at least similar characters as do the *Pupillidae*. The

<sup>29)</sup> M. Cossmann: loc. cit., IV. 1889. pag. 368.

<sup>30)</sup> M. Cossmann: loc. cit., IV 1889. pag. 368; tab. XII, fig. 35—36.

<sup>31)</sup> Cossmann: loc. cit., IV. 1889. pag. 369; tab. XII, fig. 41—42.

<sup>32)</sup> W. Wenz: Zur Systematik tertiärer Land- und Süßwassergastropoden. III. Senckenbergiana. Band II, Heft 1. Frankfurt a. M. 1920. pag. 15—18. On pag. 17.

<sup>33)</sup> A. J. Wagner: loc. cit., 1913. pag. 7.

<sup>34)</sup> Z. Frankenberger: loc. cit., pag. 228.

<sup>35)</sup> A. J. Wagner: Über die zeitliche Entwicklung der Clausiliiden und deren Beziehungen zu anderen Gruppen der Stylommatophoren. Archiv für Molluskenkunde. 53. Jahrgang. Frankfurt a. M. 1921. pag. 98—103. On pag. 102.

parallels in structure of the plicae and lamellae of the aperture which Wagner described for the *Clausiliidae*, *Pupillidae*, and *Enidae*, are not peculiar to these families, but are also found in quite a number of other families, probably belonging to the general structural plan of the aperture in the whole order. I am not prepared at present to decide definitely to which of the families of *Sigmurethra* the *Clausiliidae* are most nearly allied, but I should think that there is the greatest probability of a connection with the *Megaspiridae*. Undoubtedly this family is very old, and was already well developed during the Cretaceous. But within the then wide distributional area of the family, at present only a few remains survive. In Europe, where it is known since the Cretaceous, it became extinct during the Lower Oligocene (genus *Palaeostoa* Andr. 1884, from the Isle of Wight). But, anyhow, I should certainly regard the *Clausiliidae* as a separate family, as they form a well defined unit and, by the peculiar development of the clausal apparatus, they are, to a certain degree, isolated and well characterized within the *Stylommatophora*.

A similar origin as for the *Clausiliidae* may be claimed for the extinct genera *Filholia* Bourg. 1881 and *Rillya* Fisch. 1883. They must also be made into a separate family, *Filholiidae*, which ranks alongside with the *Clausiliidae*. These *Filholiidae* became extinct in Europe during the Lower Eocene (*Rillya* Fisch.) to the Lower Oligocene (*Filholia* Bourg.).

There is a possibility of affinities between the *Clausiliidae* and the *Urocoptidae*, *Ruminidae*, and *Coeliacidae*; but the relations of these families with the *Clausiliidae* do not appear to be very close.

It must be assumed that the earliest *Clausiliidae* had no clausilium, as it is peculiar to this family within the whole of the *Stylommatophora*, and they must have acquired it somewhere. By this clausilium the clausal apparatus of the aperture, which, as in many *Stylommatophora*, is narrowed by folds and lamellae, is highly improved and finished. In its structure it corresponds to a lamella of the wall of the aperture which has become flattened and grooved anteriorly, and remains connected with the wall of the shell only by a thin and elastic stalk. Thus the clausilium attains a certain mobility. To a certain degree this clausilium corresponds functionally to the operculum of terrestrial *Prosobranchia*, as it completes the clausal apparatus of the aperture of the shell. By further completion of its different elements the clausal apparatus of the aperture within the *Clausiliidae* has become a more and more specialized organ. The systematists of the old school, basing their studies on the shell alone, started from these deductions; O. Boettger, especially, has emphasized this in his numerous papers. I have already discussed above the view of the old school of workers who believed that the general organisation advances with the structure of the clausal apparatus of the shell; all forms with a primitive clausal apparatus had to be primitive forms. Thus a well defined system

was made from simple to highly specialized forms, from the primitive *Balea*-type to species with a highly finished clausal apparatus. But it was overlooked that in species with a primitive clausal apparatus, this may have been developed through anyone cause by reduction from a more complicated type. No difference was made between species primarily and those secondarily primitive. This mistake has only been discovered by anatomical examinations of the various species. It would even appear as if all of the known species with primitive clausal apparatus were derived from more highly organized ones, and had a simple clausal apparatus derived by reduction which, in fact, was only secondarily primitive. Primitive conditions of this kind, which are found in the rudimentary clausal apparatus of various mountain and coast forms, are distinguished by the absence of or by too a small clausilium compared with the lumen of the palate, as well as by the reduction of the lamellae of the aperture which are absent or only indicated by short and low folds. Such species are known from the most different families of *Clausiliidae*. Thus the lack of a clausilium in some forms of the subgenus *Alophia* H. and A. Ad., and of *Protoherilla* Wagn. would appear to be due to the reduction of the whole clausal apparatus within mountain forms, the ancestors of these species having possessed a clausilium. A certain progress with time in the reduction of the clausal apparatus can be observed in the Tertiary subfamily *Triptychinae*. As mentioned above the reason should be life in the hot and moist climate of the European coast regions and islands of this time. The same is true of the Tertiary genus *Eualopia* O. Bttg. which probably has no direct relation to *Alophia* H. and A. Ad., and which I have classed with the *Cochlodininae*. A living genus of the *Clausiliidae* without clausilium is *Balea* Gray, which approaches *Laciniaria* Hartm. in the structure of the genital apparatus, which is certainly not primitive, thus showing that the clausal apparatus is reduced and not primitive. I should believe the same with *Reinia* Kob. 1876, thus agreeing with H. A. Pilsbry<sup>36)</sup> who also believed that *Reinia* Kob. is not a primitive form, as von Möllendorff<sup>37)</sup> suggested, but a degenerate one. Pilsbry is right in suggesting the wellknown *Reinia variegata* A. Ad. as the secondarily simplified end of a series leading over *Reinia variegata nesiotica* Pils., and *Reinia eastlakeana* v. Möll. probably directly to typical Euphaedosoid ancestors. Thus *Reinia* Kob. stands in close relationship to the Asiatic *Cochlodininae*, especially *Euphaedusa* O. Bttg. 1877, and cannot systematically be separated from them, as has been done

<sup>36)</sup> H. A. Pilsbry: Additions to the Japanese Land Snail Fauna, IV. Proceedings of the Academy of Natural Sciences of Philadelphia. Vol. LIII. Philadelphia 1901. pag. 465—485; Pl. XXV—XXVIII. On pag. 470—473.

<sup>37)</sup> O. v. Möllendorff: Materialien zur Fauna von China. Jahrbücher der Deutschen Malakozoologischen Gesellschaft. 10. Jahrgang. Frankfurt a. M. 1883. pag. 228—269, 272—288, 356—383; Taf. 8—10. On pag. 262—265.

by Wagner and other authors. It may be mentioned, that the species of *Reinia* Kob. with a less reduced clausal apparatus, but evidently belonging to that genus, live on the Asiatic continent, in China, whereas *Reinia variegata* A. Ad. and *Reinia variegata nesiotica* Pils. are inhabitants of the Japanese Islands.

Therefore the arrangement of the forms of the *Clausiliidae* according to the structure of the aperture, from the primitive type without a clausilium to the perfect one with a highly developed clausal apparatus, is not an evolutionary series and does not correspond to the real affinities of the groups. We are not now in a position to distinguish species without a clausilium as primarily primitive forms of *Clausiliidae*, as the old school did; for in all probability the clausal apparatus in the forms known has been secondarily reduced through anyone cause. O. v. Möllendorff<sup>38)</sup> was the first who pointed out the fundamental distinction between *Balea* Gray and *Reinia* Kob., two groups closely connected by the old school. It remains for future investigation to make out the really primitive forms among the recent species; apparently they must be sought for in Asia. It remains, however, doubtful whether there remained really and primarily primitive forms without a clausilium up to the present.

These notes are bound to be only cursory, and, in many points, they are decidedly hypothetical. It has, however, been thought desirable to publish them in the present form, as a kind of general survey and as a programme for future researches. It might be useful in showing up where more detailed investigation is necessary.

### Appendix.

This publication may be followed by a systematic list of the species of *Clausiliidae* occurring in England; the extinct species are marked.

Fam. *Clausiliidae*.

Subfam. *Cochlodininae*.

*Cochlodina laminata* Mont.

Subfam. *Clausiliinae*.

*Clausilia* (*Clausilia*) *dubia* Drap.

†*Clausilia* (*Clausilia*) *pumila* C. Pfr.

*Clausilia* (*Clausilia*) *bidentata* Ström<sup>39)</sup>

<sup>38)</sup> O. v. Möllendorff: loc. cit., pag. 262—265.

<sup>39)</sup> Kennard and Woodward (A. S. Kennard and B. B. Woodward: Nomenclatorial Notes relating to British Non-marine Mollusca. Proceedings of the Malacological Society of London. Vol. XIV. London 1920. pag. 77—90. On pag. 84—85) disregarded the name *bidentata* Ström, because the original description and figure (H. Ström: Beskrivelse over Norske Insecter, Første Stykke. Det Trondhiemske Selskabs Skrifter. III. Deel. Kjöbenhavn 1765. pag. 376—439. Tab. VI. On pag. 436; tab. VI, fig. 17) might equally apply to another form. I am not of their opinion. Indeed, Ström's description and figure of *bidentata* Ström are incomplete enough. But I think that for Ström no other species was in question, the



- † *Clausilia* (*Clausilia*) *parvula* Stud.  
 † *Clausilia* (*Iphigena*) *ventricosa* Drap.  
*Clausilia* (*Iphigena*) *rolphii* Gray.  
*Laciniaria* (*Laciniaria*) *biplicata* Mont.  
*Balea perversa* L.

*Clausiliidae incertae sedis.*

- † *striatula* E. Edw.  
 † *pliocena* S. V Wood.

It will be seen that certain species still existing on the Continent have been living on the British Islands, but have become extinct later. When, previous to the Great Ice Age, a dryer climate prevailed in Western Europe, eastern forms, under more favourable conditions, extended to the Atlantic and outposts, among others the East European *Clausilia* (*Clausilia*) *pumila* C. Pfr., had even reached England. At present this species has entirely disappeared again from Western Europe and only ranges as far west as the Danish Islands and from there southward through Germany east of a line Hamburg—Eisenach—Würzburg—Regensburg. Of course a change of climate also destroyed further species. But while on the Continent the devastated regions were repopulated during the Interglacial spaces when a repeated change of retreat and advance of one species in the same country can be observed, the isolation of England had been effected and was an unsurmountable barrier to reimmigration. It is therefore that the Clausiliid fauna of the British Islands with its 6 living species is poor compared to the corresponding ones on the Continent. Apparently this process of pauperisation of the British Clausiliid fauna is still going on; it is generally acknowledged that f. i. *Laciniaria* (*Laciniaria*) *biplicata* Mont. becomes rapidly extinct. In a country whose fauna is so well controlled as regards mollusks as England, this case decidedly deserves attention. *Laciniaria* (*Laciniaria*) *biplicata* Mont. would appear to be an advanced western outpost, early and widely spread over great parts of Europe, of a group, originally at home in the southeast of Europe, and the countries round the Black Sea where its principal types and the bulk of its species are still abundantly represented.

*Clausilia* (*Iphigena*) *plicatula* Drap. mentioned by S. V. Wood<sup>40)</sup> as occurring in the Upper Pliocene Coralline Crag of

figure obviously showing a true *Clausilia* sens. strict. I therefore do maintain *bidentata* Ström. Kennard and Woodward have also identified *bidentata* Ström with *Clausilia* (*Clausilia*) *rugosa* Drap. It would appear to me that *rugosa* Drap. (Pyrenees, S. France, N. and C. Italy) is the southwestern representative of a group of which *bidentata* Ström is the northern type. In this opinion I agree with A. Schmidt, O. Boettger, and C. A. Westerlund. It remains for future research to ascertain whether *rugosa* Drap. and *bidentata* Ström should be regarded as separate forms or subspecies of the same species. The name *nigricans* Mat. and Rack. is a synonym of *bidentata* Ström.

<sup>40)</sup> S. V. Wood: A Monograph of the Crag Mollusca. II. pag. 307.

Copford is, according to A. H. Cooke<sup>41)</sup>, a misidentification for *Clausilia (Iphigena) rolphii* Gray.

As regards the species *pliocena* S. V. Wood<sup>42)</sup>, I cannot give a definite opinion, but I do not believe it to be a separate extinct species. Most probably it is a species still occurring on the Continent but extinct in England, or it may even be a recent or fossil British species. It would be a good thing for a British malacologist to examine Wood's type in the British Museum in order to ascertain the exact status of this form. It further remains to be proved whether the specimens of „*pliocena* Wood“ mentioned by Loricé<sup>43)</sup> from the Amstélien (Upper Pliocene) of Diemerbrug, Holland, really belong here; judging from the locality it is quite possible.

Finally, it remains for an English student, to settle the systematic position of the species *striatula* F. Edw.<sup>44)</sup> from the Bembridge Beds, Isle of Wight, of which I have not seen an actual specimen. It would appear to belong to the *Cochlodininae*, and is possibly a member of one of the Early Tertiary genera of this family, which have been discussed above.

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<sup>41)</sup> A. H. Cooke: loc. cit., pag. 253.

<sup>42)</sup> S. V. Wood: Supplement to the Monograph of the Crag Mollusca, with Descriptions of Shells from the Upper Tertiaries of the East of England. Palaeontographical Society. Vol. XXVIII. 1874. pag. 188; tab., fig. 22.

<sup>43)</sup> J. Loricé: Contributions à la Géologie des Pays-Bas. Mémoires de la Société belge de Géologie, de Paléontologie et d'Hydrographie. Tome III. Bruxelles 1889. pag. 409—449. On pag. 435, 437.

<sup>44)</sup> F. E. Edwards: A Monograph of the Eocene Mollusca, or Description of Shells from the Older Tertiaries of England. Palaeontographical Society. Part II. 1852. pag. 79; tab. X, fig. 6a—b.

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