HOMEOMORPHY, AND A REMARKABLE ILLUSTRATION.

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ABSTRACT. The phenomenon of homeomorphy is briefly considered and the wider usage of the term in preference to the commonly misused word "mimicry" is urged. Some typical examples of homeomorphy are cited and the remarkable heterochronous brachiopod homeomorphs *Tetractinella* and *Cheirothyris* are discussed and illustrated.

HOMEOMORPHY is one of the severest impediments to the clarification of genetic relationships in any group of organisms. It is best defined as the phenomenon of general superficial resemblance but dissimilarity in particular structural detail. Homeomorphy may occur in or between taxonomic brackets of any order; for, as Buckman says, "It is the tendency of different genetic stocks to pass, quite independently, through similar phases of development" (1901, p. 231).

The word homeomorphy bears none of the eugenic or teleological implications attached to the term mimicry which, if it can be proved, should probably be regarded as a special case of homeomorphy or of "protective coloration." In some instances of so-called mimicry the mimic and the model are known to have more or less different ecologic ranges or different habits that would allow an alert predator readily to distinguish between them, or they may even occur in entirely different geographic regions. For instance, Austin H. Clark says that, "In the often cited North American case of the Viceroy butterfly (*Basilarchia archippus*) which allegedly mimics the supposedly nauseous Monarch (*Danais plexippus*); the Viceroy keeps to the immediate vicinity of trees or bushes, especially on hillsides; whereas the Monarch is preëminently a butterfly of open country, particularly of flat country, and seldom goes near trees except to roost in them at night. The flight of the two is quite different and they are easily distinguished at any distance."[1]

The idea of homeomorphy, and the word, were introduced—to the best of my knowledge—by S. S. Buckman (1895, p. 456), in stressing the distinction between closely similar species which

[1] Clark, Austin H.: Communication in a letter dated March 31, 1941.

were not homogenetic. As a homely illustration of this distinction one might say that identical twins are homogenetic, whereas unrelated "doubles" are homeomorphous but not homogenetic. Actually, of course, this illustration is inaccurate, for the "doubles" in question are conspecific and therefore homogenetic in Buckman's sense. In paleontologic usage the time element is dealt with by referring to similar but unrelated species which occur at the same stratigraphic horizon as isochronous homeomorphs, while similar but genetically unrelated forms occurring at different levels in the geologic column are called heterochronous homeomorphs (Buckman, 1895, p. 458).

Besides Buckman, many other paleontologists have added to our knowledge of homeomorphy by discussion of the concepts involved and by the recording of examples. In North America A. Hyatt, J. P. Smith, C. Schuchert, G. A. Cooper, and others have made important contributions in this respect. Examples of homeomorphy could be multiplied far beyond the needs of illustration. Striking and well known instances are the resemblance of the operculate Silurian and Devonian "slipper coral" *Calceola* to a brachiopod, of the peculiar Permian brachiopod *Leptodus* to a fish tooth, of the Cenozoic and Recent vermiculariid snail shells to those of serpulid worms, and of the Cretaceous rudistid pelecypods and the Permian richthofeniid brachiopods to various cup-corals. Austin H. Clark has furnished some interesting examples in the Recent insects; writing that the larvae of the fly *Microdon* have twice been described as limpets, the larvae of the moth *Apteroma* build spiral cases extremely like the helicoid snail shells, and the larvae of the caddis-fly *Helicopsyche* builds spiral cases of sand grains resembling snail shells.[2]

Within such groups as the cephalopods and brachiopods homeomorphy is commonly so subtle that only the specialist can appreciate it. Ordinarily, however, distinctions can readily be seen, once discovered, as in the case of the three-way homeomorphy between the punctate shelled brachiopod *Pionodema* and the impunctate *Doleroides* and *Mimella* (Cooper, 1930).

One of the most interesting and unusual examples of homeomorphy on record is that between the fantastically tetraplicate brachiopod genera *Tetractinella* Bittner (Pl. 1, figs. 1-4, 8) and *Cheirothyris* Rollier (Pl. 1, figs. 5-7, 9-12). *Tetrac-*

[2] Clark, Austin H.: Letter dated April 1, 1941.

tinella is a Middle Triassic genus with a spiral brachidium and an impunctate shell, whereas *Cheirothyris* is an Upper Jurassic genus with a loop for a brachidium and a punctate shell. These heterochronous homeomorphs belong to entirely different stocks, distinct since at least late Silurian time, yet they resemble one another so closely in general external expression that they have been commonly mistaken for a single species from 1820 (Schlotheim) to the present day. Von Buch (1834) described the two genera as a single species, recording such peculiarities of form and ornamentation that one is astonished to find that the description readily fits either of these remarkable genera. Indeed there is more superficial dissimilarity between immature and adult specimens in either genus than there is between representatives of the two genera at the same stage of growth, for the relative position of the four plicae with respect to one another and the ends of the shell changes with growth.

Actually there are fairly conspicuous external differences by which the rostrospiroid *Tetractinella* and the terebratuloid *Cheirothyris* can be separated. They are apt to be overlooked merely because the peculiarity of gross form is such that, from the first glance, one is under the psychological disadvantage of preconviction that such unique morphology is not likely to be duplicated. The ventral beak and pedicle foramen of *Cheirothyris* are much larger than the same structures in *Tetractinella* and the former has a punctate, the latter an impunctate shell.

There is no need to stress the pitfalls of homeomorphy—they are obvious. On the other hand this phenomenon may be of great value in solving problems more important than the rectification of a few generic names. Probably some instances of homeomorphy are purely fortuitous; others may represent ecologic responses. It is commonly said that the richthofeniid brachiopods resemble cup-corals because they lived in a reefy environment; yet few corals are associated with the richthofeniids, and many other brachiopods that were entombed in even more demonstrably reefy strata do not resemble corals. Surely the problem of the relationship, if any, of homeomorphy to environment merits careful analysis; but before such analysis can be made we must have abundant data on the paleoecology of our homeomorphs.

Genus *Tetractinella* Bittner, 1890.

Plate 1, figs. 1-4, 8.

Genotype: *Terebratulites trigonellus* Schlotheim, 1820; emend. d'Orbigny, 1850.

Discussion: When Hall and Clarke (1894) selected *Terebratulites trigonellus* Schlotheim as the genotype of *Tetractinella* they perpetuated an aggravating source of confusion. The matter of what *Tetractinella* is then became dependent on what Schlotheim's species was, and there is evidence to show that, when his description was being written, Schlotheim had at hand two species belonging to two genera. Schlotheim states that his species is not uncommon in the Jurassic limestones, yet he cites it also from Fredericks quarry at Tarnowitz, in Silesia, a Middle Triassic (Muschelkalk) horizon, and makes reference to figures illustrating the Triassic form (Quenstedt, 1868, p. 281). D'Orbigny (1850) recognized the confusion, having seen specimens from Tarnowitz in the collections of de Verneuil (*fide* Quenstedt, 1868, p. 285), and proposed the name *Terebratella fleuriausa* for the Upper Jurassic forms. Quenstedt (1868) gave an excellent discussion of the characters of the punctate, long-looped Upper Jurassic shell involved but did not make clear exactly what he proposed to call it, using the specific name *trigonella* in a provisional sense. Bittner apparently accepted d'Orbigny's conclusions, for he regarded Schlotheim's species as an impunctate, spire-bearing Middle Triassic shell. The least confusion is occasioned by accepting d'Orbigny's emendation as Bittner did. If Schlotheim's collections are still extant, a holotype for the species *Tetractinella trigonella* (Schlotheim) should be selected from among the specimens from Tarnowitz; otherwise a neoholotype should be established on a specimen from that locality.

The name *Trigonella* Quenstedt (1868) in no way interferes with Bittner's *Tetractinella* inasmuch as it is a homonym (Schuchert and LeVene, 1929, pp. 87, 125) and never had any other taxonomic status.

Neotrigonella Cossmann (1910) is either a *nomen nudum* or a homonyn of *Tetractinella*. The name was proposed by Cossmann to replace "*Trigonella* Buckman 1907 (Brachiopode, Quart. Journ., Vol. 63) *non* Conrad, 1837." Buckman proposed *Trigonellina* in this reference but not *Trigonella*, so it is doubtful if Cossmann's name can be said to replace anything.

If *Neotrigonella* is regarded as a new name for *Trigonella* Quenstedt, the genotype of the homonym *Trigonella* becomes, *ipso facto*, the genotype of *Neotrigonella* Cossmann. That species is, by monotypy, *Terebratulites trigonellus* Schlotheim = *Tetractinella trigonella* (Schlotheim), the "*Trigonella suevica*" Schröter 1782 mentioned by Quenstedt (1868, p. 25) being non-binomial (see also Dall, 1877).

Genus *Cheirothyris* Rollier, 1919[3]

Plate 1, figs. 5-7, 9-12.

Genotype: *Terebratella fleuriausa* d'Orbigny, 1850.

Discussion: The genus *Cheirothyris* includes the punctate, long-looped, quadriplicate Upper Jurassic shells such as occur, among other localities, at Nattheim, Leidenheim, and Dietingen, in Germany. Under the homonymous name of *Trigonella*, the generic characters of this terebratuloid were discussed at length by Quenstedt (1868) and no present warrant is seen for amplification of that description. D'Orbigny's description of *Terebratella fleuriausa* makes it clear that he dealt with a quadriplicate Jurassic terebratuloid, and, even if the specimens generally considered to be *Cheirothyris fleuriausa* should prove to be a different species, the genus probably will not be affected.

Under the discussion of *Tetractinella* (above) it is shown that *Neotrigonella* Cossmann is either a *nomen nudum* or a homonym. In either instance it cannot impair the validity of *Cheirothyris*.

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[3] Rollier's paper was not seen by me but the generic name *Cheirothyris*, with citation of the genoholotype, is given by Schuchert and LeVene (1929, p. 40). This generic name was called to my attention by Dr. G. A. Cooper.

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PLATE I*

Figs. 1-4, 8. *Tetractinella trigonella* (Schlotheim).
Dorsal, ventral, lateral, posterior, and anterior views (x1). Middle Triassic; Recoaro, northwest Vicenza, Italy.

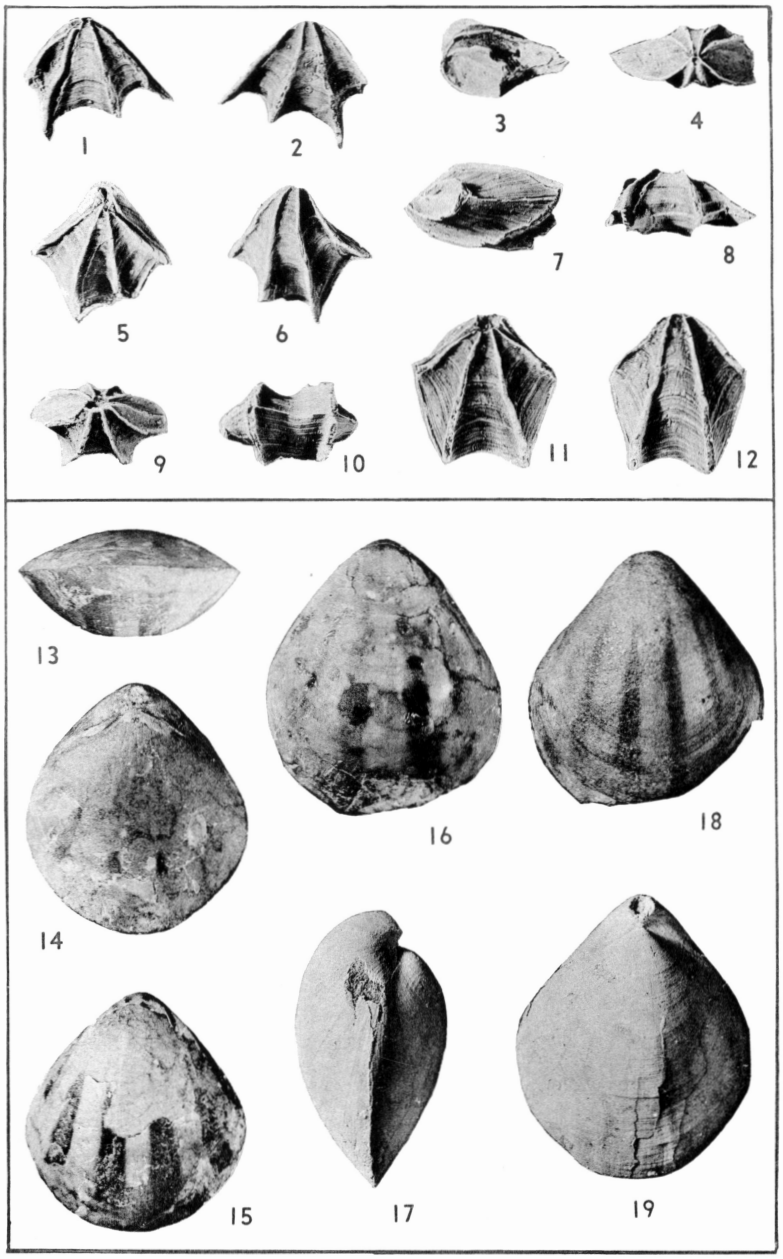
Figs. 5-7, 9-12. *Cheirothyris fleuriausa* (d'Orbigny).
5-6. Dorsal and ventral views (x1) of a small specimen for comparison with Figs. 1-2. Upper Jurassic (White Jura); Nattheim, Wurtemburg, Germany.
7, 9-12. Lateral, posterior, anterior, dorsal and ventral views (x1) of a large specimen. Upper Jurassic; Leidenheim, Wurtemburg, Germany.

Figs. 13-15. *Cranaena thomasi* Stainbrook.
Anterior, dorsal, and ventral views (x2) of a fine specimen. Upper Middle Devonian, Cedar Valley formation, lower part of Linwood member (Atrypa independensis zone); small quarry at west edge of Solon, Iowa.

Fig. 16. *Cranaena littletonensis* Stainbrook.
Ventral view (x3) of a specimen showing brownish red, radial color bands. Upper Middle Devonian, Cedar Valley formation, upper part of Littleton member (Atrypa waterlooensis zone); Fayette, Iowa.

Figs. 17-19. *Cranaena cooperi* Cloud, n. sp.
17, 19. Lateral and dorsal views (x1½) of the holotype.
18. Ventral view (x1½) of a paratype.
Specimens from upper Middle Devonian, Milwaukee formation, Lindwurm member, Milwaukee cement quarry, Berthelet, Wisconsin.

* The specimens represented by Figures 1-12 are from the Schuchert Brachiopod Collection, Peabody Museum, Yale University; those by Figures 13-19 are the property of the U. S. National Museum. Except for Figs. 13-16 and 18, the specimens were coated with ammonium chloride before being photographed.



HOMEOMORPHY—COLOR-PATTERNS