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The chromosomes of *Catinella arenaria* (Bouchard-Chantereaux, 1837) with a review of the cytological conditions within the genus *Catinella* and considerations of the phylogenetic position of the Succineoidea[1]) ord. nov. (Gastropoda: Euthyneura)

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ABSTRACT

The cytological conditions in the genus *Catinella* are discussed. The haploid chromosome number of *Catinella arenaria* is 6. The karyotype morphology differs from other known Catinellinae by the position of the centromeres and the chiasma frequency. The subgeneric characters of the group are surveyed in detail with respect to their phylogenetic value. The unique phylogenetic position of the Succineidae is pointed out and a new order Succineoidea is proposed.

INTRODUCTION AND ACKNOWLEDGEMENTS

In one of our previous papers we have demonstrated the feasibility of the taxonomic separation of closely allied gastropod species with numerically equal chromosome complements by the application of comparative cytotaxonomical methods (Butot & Kiauta, 1966). The present study of chromosomes in *Catinella (Quickella) arenaria* has given us the opportunity to review the cytotaxonomical conditions within the genus of which six species have so far been examined cytologically (table I). Five of these have a numerical equal chromosome complement but to the best of our knowledge no figures of *Catinella texana* or of *C.* cf. *oregonensis* chromosomes have been published.

We acknowledge thankfully the kind cooperation of Dr. R. E. Baker (The Nature Conservancy, Furzebrook Research Station near Wareham, Great Britain), who provided us with a number of specimens of *C. arenaria*, collected in September, 1966 at Braunton Burrows, Devon, and of Dr. M. R. Honer (Wageningen, The Netherlands), who read the manuscript.

Preparations of *C. arenaria* were made from November 9th to 14th, 1966.

[1]) The name has been used by Baker, 1963, Proc. Acad. Nat. Sci. Philad. 115 (8): 215, to indicate a superfamily in his suborder Heterurethra.

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TABLE I. Chromosome numbers in *Catinella*

species	chrom. numbers n	chrom. numbers 2n	locality	reference
Catinella (Catinella) rotundata (Gould, 1848)	5	10	Hawaii	Burch, 1964b
C. (Mediappendix) cf. *gabbi* (Tryon, 1866)	6	12	California	Burch, Patterson & Natarajan, 1966
C. (Mediappendix) cf. *oregonensis* (Lea, 1841)	6		California	Burch & Patterson, 1965
C. (Mediappendix) texana (Hubricht, 1961)	6	12	Southern USA	Patterson & Burch, 1966
C. (Mediappendix) vermeta (Say, 1824)	6	12	Michigan	Burch, 1964a
C. (Quickella) arenaria (Bouchard-Chantereaux, 1837)	6	12	England	this paper

All induviduals were rather young, and most of them in the very beginning of spermatogenesis. In seven specimens the various divisional stages could be studied. Fully developed spermatozoa were, however, very scarce. In all, 71 microphotographs were made.

Ovotestes in active stages of gametogenesis were examined. The tissues were fixed and stained by the lacto-acetic-orceine squash technique (Boyes & van Brink, 1964). The slides were studied using a Wild phase contrast microscope, 100 x oil immersion objective, 10 x oculars, factor 1.25 and photographed on Agfa IFF panchromatic film. The figures in this paper are printed at a magnification of 1750.

THE CHROMOSOMES OF *Catinella (Quickella) arenaria*

The diploid chromosome number of *C. arenaria* is 12. The six pairs can be discerned easily in the spermatogonial cells (pl. I, pl. II fig. 1). The centromere position is either submedian, nearly median or subterminal. No structural pecularities could be found in the mitotic metaphase chromosomes but for an occasionally deeper stained terminal section on one arm of one or both longest chromosomes (pl. I). The chromosome size varies at this stage between 9 and 2.6 μ, approximately.

In early diakinesis the bivalents appear as circles, crosses and rods of varying sizes. In *C. arenaria* the appearance of at least two bivalents (rods and crosses) suggests a single chiasma, whereas three or four have probably two chiasmata per bivalent (rings). One pair has a pronounced delayed pairing (pl. II fig. 3). At metaphase II the diads appear as "dumb bells" or paired "dumb bells". They are about half the size of the spermatocyte I bivalents (pl. II fig. 4).

The cytological picture of *Catinella arenaria* is unique among the hitherto examined species of the genus of which microphotographs have been published. This feature is stressed by (1) the position of the centromere, which lies in *C.* cf. *gabbi*, *C. rotundata* and *C. vermeta* always medianly or submedianly, and by (2) the chiasma frequency.

Since *C. rotundata* differs clearly from other species of the genus by its lower chromosome number and no figures were available of the chromosomes of *C. texana* and *C.* cf.*oregonensis*, the centromere position of the remaining three species is tabulated in table II. The data for *C. vermeta* and *C.* cf. *gabbi* were compiled from drawings published by Burch (1964 a), Patterson & Burch (1966) and Burch, Patterson & Natarajan (1966) respectively. Contrary to these authors we considered in table II chromosomes as metacentrics only in the case of the arm ratio being 1 : 1.

TABLE II. Centromere position (constriction) in chromosomes of *Catinella* spp.

Pair	Species		
	arenaria	cf. *gabbi*	*vermeta*
1 st	submedian	submedian	submedian
2 nd	nearly median	submedian	submedian
3 rd	submedian	median	submedian
4 th	nearly median	submedian	submedian
5 th	subterminal	submedian	submedian
6 th	subterminal	submedian	median

Although it is often difficult to determine a construction as median or submedian, submedian or subterminal, the smallest two pairs in *C. arenaria* are quite plainly subacrocentric (pl. I, Karyograms), and differ in this feature essentially from the other n = 6 *Catinella* species.

An heterochromatic terminal region in one chromosome arm of the longest pair in *C. arenaria* is also interesting. Burch (1964 a) has described a secondary constriction in one arm of one of the longest chromosomes in *C. vermeta.* In *C.* cf. *gabbi* no structural pecularities are apparent (Burch, Patterson & Natarajan, 1966).

In *C.* cf. *gabbi* the bivalents are "mostly all" in the form of crosses, indicating only one chiasma per bivalent (Burch, 1964 a), however, Patterson & Burch (1966) record a multiple loop-shaped bivalent with three chiasmata. In *C. arenaria,* on the other hand, the appearance of at least two bivalents suggests a single chiasma, whereas the remaining chromosomes have probably two chiasmata per bivalent.

DISCUSSION

The genus *Catinella* Pease, 1870 is divided into three subgenera: *Catinella* s. str., type *Succinea rubida* Pease, 1870; *Quickella* Boettger, 1939, type *Succinea arenaria* Bouchard-Chantereaux, 1837; and *Mediappendix* Pilsbry, 1948, type *Succinea campestris vagans* Pilsbry, 1900. The subgenera are recognized by a penial appendix which is lacking in *Catinella* s. str.; indistinct and existing only as a rudiment in *Quickella;* well developed and protruding from the middle of the penis in *Mediappendix* (Odhner, 1950).

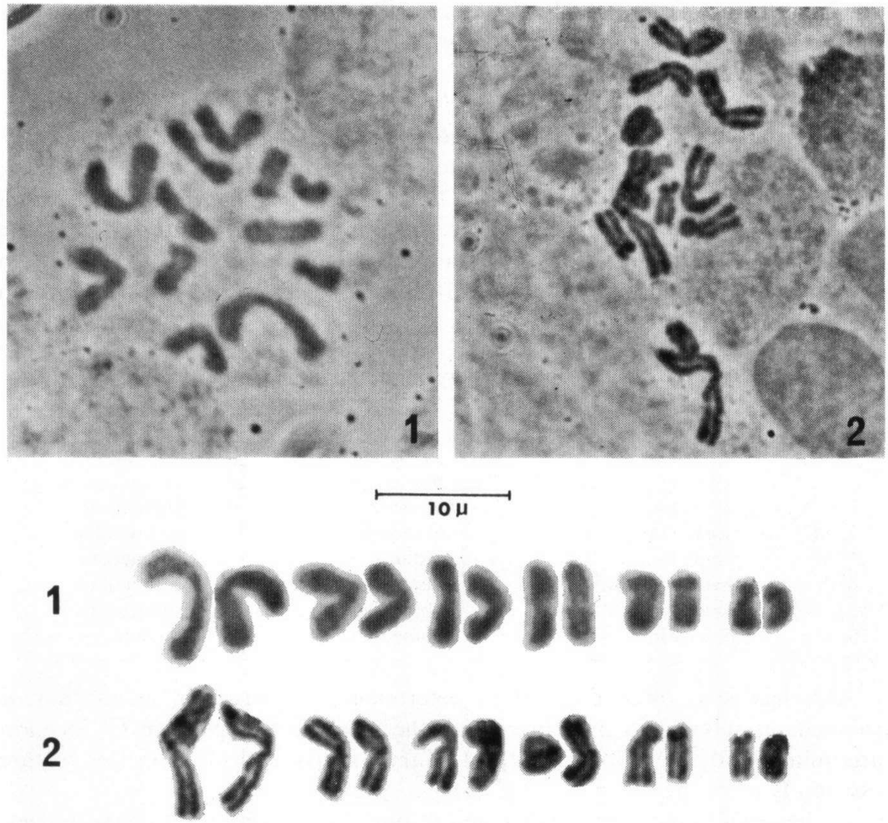

PLATE I. *Catinella arenaria*: spermatogonial metaphase and karyograms (× 1750).

TABLE III. Phylogenetically important anatomical characters in *Catinella*

subgenus	shell whorls	radula marginals and laterals	radula number of teeth in horizontal row	appendix	vagina	length truncus bursae	n
Catinella	1½—2	not primitive	115—123	none	short	equals penis length	5
Quickella	3½—4	greater antiquity than Mediappendix	29— 41	hardly developed	longer	twice penis length	6
Mediappendix	2½—3	primitive	45— 51	well developed	longer	exceeds penis length	6

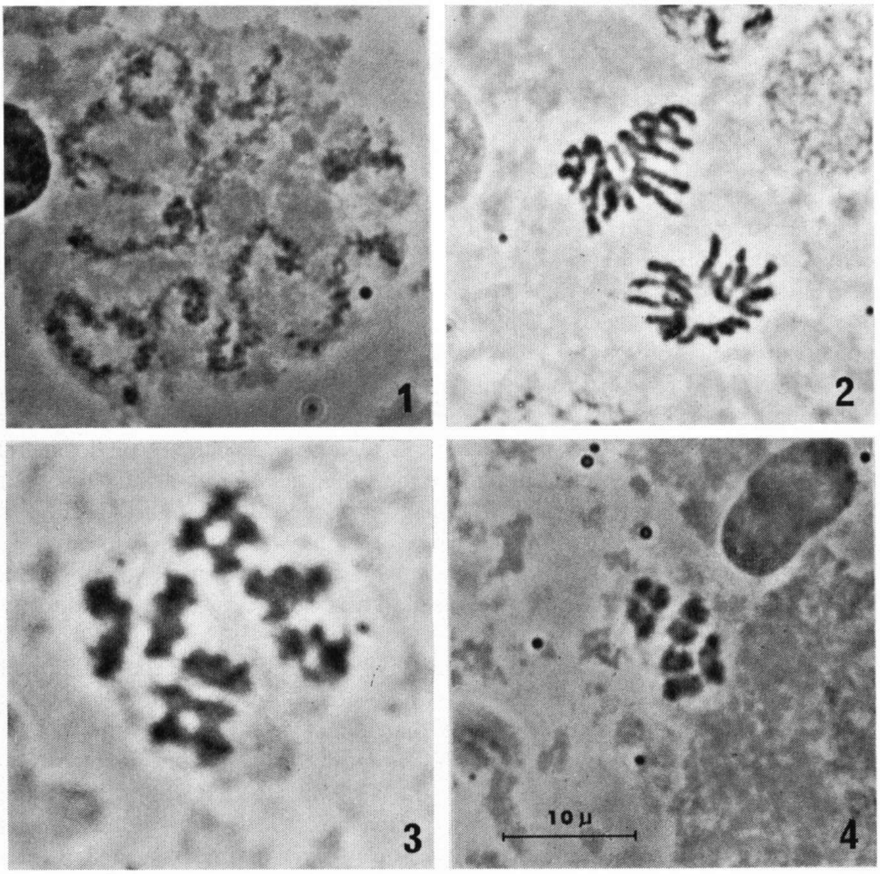

PLATE II. *Catinella arenaria*: mitotic and meiotic stages: 1, early spermatogonial prometaphase; 2, late spermatogonial anaphase; 3, early spermatocyte metaphase I (polar view); 4, spermatocyte metaphase II (polar view) (× 1750).

In table III six morphological characters are tabulated. They are of a definite subgeneric importance. For three of them their relative primitivity is discussed by Odhner (1950).

1. Conchologically ear shaped shells are considered more advanced than shells with a high spire, which consideration points to *Catinella* s. str. as to the most advanced subgenus and to *Quickella* as the most primitive one.
2. *Quickella* and *Mediappendix* preserved in their broad marginals of the radula a more primitive condition than the radula of *Catinella* did, while *Quickella* in the ectocones of the laterals preserved a trace of greater antiquity than *Mediappendix*.
3. The number of teeth in the horizontal rows of the radula is considered to decrease with increased specialization, consequently *Catinella* is the most primitive and *Quickella* the most advanced subgenus in this respect.
4. The phylogenetic value of the penial appendix is unclear. It is well develop-

ed in *Mediappendix* and it is reduced in *Quickella*. In *Catinella* the penial appendix is completely lacking but it is not clear whether this condition is primary (primitive) or secondary (specialized).

5. The vagina in *Catinella* is clearly shorter than in *Quickella* and *Mediappendix* but no difference as to its length is found between the two latter subgenera.
6. The length of the truncus bursae in *Catinella* equals the penis length. It is longer than the length of the penis in *Mediappendix* whereas it reaches twice the penis length in *Quickella*.

From the above is clear that *Mediappendix* occupies an intermediate position between the subgenera *Catinella* and *Quickella* in the following aspects: number of shell whorls, characters of marginals and laterals, number of teeth in the horizontal row of the radula and in the length of the truncus bursae. The length of the vagina and the chromosome number do not contradict this evidence, although they are similar in *Quickella*. Whatever phylogenetic value is assigned to the penial appendix the subgenus *Mediappendix* does not take an intermediate position, it is either most specialized if the absence of the penial appendix is a primitive character or most primitive if its absence is a result of reduction. It is not clear which of the remaining two subgenera should be considered the most specialized. The evidence in table III does not permit a conclusion.

Butot (1967) has shown that in the phylum Mollusca a general parallel exists between specialization and increase of chromosome number. If this were true *Catinella* is more primitive than *Quickella*. This is supported so far by a high number of teeth in the horizontal row of the radula only. Additional support could be given by the lack of a penial appendix. If the latter condition is primary, the short vagina and the length of the truncus bursae are most likely also primitive features. The number of shell whorls and the nature of the marginals and laterals of the radula, however, are not primitive.

The male genital organ of the genera *Quickia* and *Indosuccinea* in Catinellinae according to Odhner (1950) represent the most archaic type in any of the Catinellinae. If this were true *Catinella* is also more primitive than *Quickella*. The development of penial appendages is in such a case phylogenetically a sign of progressive evolution. For this reason cytological studies of *Quickia* and *Indosuccinea* would be most desirable.

The systematic position of Succineidae

In Succineidae the Catinellinae are generally accepted more archaic when compared to the Succineinae. Their haploid chromosome numbers vary from 5-6 and from 12-22 respectively. The same holds true for Heterurethra compared to the remainder of Stylommatophora, chromosome numbers varying from 5 to 22 and from 20 to 34 respectively, in haploid cells. These numbers form distinct series.

In Succineidae features are found atypical of the constituent orders of

"Pulmonata". They resemble basommatophorans in the broader bases of the tentacles, the discrete prostate, the occurrence of a posterior gastric coecum, their egg capsules bound together in the spawn, and a caudal vesicle not being visible during the embryonic period (Rigby, 1965). The reproductive system differs from that of Basommatophora and agrees with the pattern of opisthobranch systems. The Succineidae are more advanced than the marine tectibranchs. Rigby (1965) concluded with reference to the anatomy of alimentary and reproductive systems and to cytological features that the Succineidae are more properly placed among the "opisthobranchs" than among the Stylommatophora. The classification in the Anaspidea (= Aplysiacea) is supported by the resemblance of the alimentary and reproductive systems.

Cook (1966) studied the central nervous system of *Succinea putris*. *Succinea putris* resembles the Basommatophora in the presence of a group of chrome-hematoxylin positive cells lying under the medio dorsal bodies, the presence of a lateral lobe, the structure of the medio dorsal bodies and the lack of cerebral commisure nerves. In other features, however, *S. putris* resembles the other Stylommatophora much more than it does "Opisthobranchia", it even has typical stylommatophoran features. Therefore reclassification of *S. putris* as a basommatophoran or an opisthobranch on the basis of the morphology of the central nervous system, is not warranted.

Because of the Succineidae are pulmonates with the eyes at the tips of the dorsal tentacles, it would seem logical to regard them as Stylommatophora. Other stylommatophoran "pulmonates" with the eyes at the tips of the dorsal tentacles: the families Onchidiidae, Rathouisiidae and Veronicellidae have been removed from Stylommatophora as a separate order Soleolifera within Euthyneura. Because of the position of the eyes in Succineidae it seems illogical to place the family in Basommathophora. The position at the base of Stylommatophora seems improbable, as the family, especially in the elasmognathous jaw, shows an homogenity which prevents any phylogenetical relationship to the remainder of Stylommatophora. The family is really remarkable and unique. In fact the origin of the Stylommatophora is uncertain as they cannot be derived from Ellobiidae in Basommatophora as is generally accepted. This family, though primitive basommatophorans, are already too far entrenched in typical basommatophoran characteristics to be possible ancestors of the Stylommatophora (Rigby, 1965). Therefore, the position of Heterurethra at the base of Stylommatophora is most uncertain.

It is clear that Heterurethra cannot be identified with one of the existing euthyneuran orders. No other group shows a combination of stylommatophoran, basommatophoran and tectibranch features. As is done with the Soleolifera, the Heterurethra should be removed from Stylommatophora forming a separate order under the name of Succineoidea [1]). The older names Elasmognatha and Heterurethra for this group are rejected as we prefer to follow Taylor & Sohl (1962).

[1]) The name has been used by Baker, 1963, Proc. Acad. Nat. Sci. Philad. 115 (8): 215, to indicate a superfamily in his suborder Heterurethra.

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