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Klepton and Synklepton: Two New Evolutionary Systematics Categories in Zoology

By ALAIN DUBOIS and RAINER GÜNTHER

Abstract

The aim of this paper is to provide a general name and nomenclatural rules for some particular animal "forms" which cannot properly be considered as "biological" species, such as gynogenetic and hybridogenetic unisexual fish of the genus *Poeciliopsis*, gynogenetic unisexual fish of the genus *Poecilia*, gynogenetic unisexual salamanders of the genus *Ambystoma*, and hybridogenetic (or leaky hybridogenetic) frogs of the genus *Rana*. All these forms, despite their diversity, have the following features in common: they are of hybrid origin; their heredity is clonal or hemiclonal; for their reproduction, such forms depend on the gametes of a distinct "good" species. To accommodate these forms, we suggest the general name klepton, and we propose to call synklepton a group consisting of two or more "good" species and one or more kleptons issued from the hybridization of these species. We suggest to consider kleptons as taxa of the species-group, belonging to a third taxonomic category distinct from both the categories species and subspecies. Kleptic names should therefore follow the same nomenclatural rules as specific or subspecific names. We propose a uniform mode of notation for kleptons and synkleptons. Kleptons members of a synklepton should be given names such as *Rana* (synkl. *esculenta*) kl. *esculenta* LINNAEUS, 1758 or, more shortly, *Rana* kl. *esculenta*, while the "good" species belonging to the same synklepton should bear names such as *Rana* (synkl. *esculenta*) *lessonae* CAMERANO, 1882 or, more shortly, *Rana* *lessonae*.

Introduction

During the last 20 years, evolutionary zoologists have discovered several particular situations, in which a given "form" subsists in nature only thanks to a kind of "sexual parasitism": for their reproduction, such forms need the gametes of another form or species. In the present paper we shall limit ourselves to cases known among vertebrates. Similar examples may exist in invertebrates but need further study. The purpose of this paper is twofold: (1) to provide a general term for calling these forms; (2) to suggest rules for their nomenclature.

1. Some examples

1.1. Hybridogenetic and gynogenetic fish

The American fish genus *Poeciliopsis* (Cyprinodontiformes, Poeciliidae) contains several "normal" bisexual species, among which *Poeciliopsis occidentalis* (BAIRD and GIRARD, 1853), *Poeciliopsis latidens* (GARMAN, 1895), *Poeciliopsis lucida* MILLER, 1960, *Poeciliopsis monacha* MILLER, 1960 and *Poeciliopsis viriosa* MILLER, 1960, and several

unisexual all-female "forms". These unisexual forms have been the matter of numerous research works (see review up to 1977 in SCHULTZ 1977; and see also VRIJENHOEK 1978; LESLIE and VRIJENHOEK 1978; ANGUS and SCHULTZ 1979; MOORE and EISENBREY 1979; BULGER and SCHULTZ 1979, etc.). These forms prove to be of two kinds.

One kind may be exemplified by the form which SCHULTZ (1969) has called *Poeciliopsis monacha-lucida*. This unisexual form is diploid and originated by hybridization between *Poeciliopsis monacha* and *Poeciliopsis lucida*. During the meiosis of these females, the paternal (*lucida*) genome (genome = one chromosome set) is eliminated as a whole, and all the gametes which are produced contain a pure *monacha* genome. The eggs of these females are fertilized in nature by sperm from *P. lucida* males, and thus at each generation genotypes and phenotypes are restored which are identical to those of F1 hybrids between *P. lucida* and *P. monacha*. Such hybrid forms can therefore reproduce and survive only through back-crossing at each generation with one of the parental species from which they issued. SCHULTZ (1969) created the term "hybridogenesis" to call the particular reproductive mode of such hybrid forms.

A second kind of unisexual forms exists in the genus *Poeciliopsis*. Such forms are triploid. One of them possesses 2 genomes from the species *P. monacha* and one from the species *P. lucida*; another one has 2 genomes from *P. lucida* and one from *P. monacha*. SCHULTZ (1969) proposed to call them respectively *Poeciliopsis 2 monacha-lucida* and *Poeciliopsis monacha-2 lucida*. These forms are clearly of hybrid origin, and seem to have arisen through the fertilization of unreduced diploid gametes bearing one set of *lucida* and one set of *monacha* chromosomes, such as are sometimes produced by females of *P. monacha-lucida*, by normal sperm of *P. lucida* or of *P. monacha*. These triploid females produce unreduced triploid gametes which are stimulated to develop, but not truly fertilized, by foreign sperm and therefore give birth to gynogenetic offspring. Activation of these eggs is effected by sperm from one of the two parental species: *P. monacha* in the case of *P. 2 monacha-lucida*, and *P. lucida* in the case of *P. monacha-2 lucida*.

A rather similar situation has been reported in the related genus *Poecilia*, which includes a diploid "form", known as *Poecilia formosa* (GIRARD, 1859), issued from the hybridization between the "good" species *Poecilia latipinna* (LESUEUR, 1821) and *Poecilia mexicana* STEINDACHNER, 1863, and a triploid form, still unnamed, which possesses two sets of chromosomes from *P. mexicana* and one from *P. latipinna*. Both these hybrid forms reproduce by gynogenesis (see review in SCHULTZ 1977 and see also TURNER, BRETT, RASCH and BALSANO 1980).

1.2. Gynogenetic salamanders

The American salamander genus *Ambystoma* (Urodela, Ambystomatidae) includes many "normal" bisexual species, among which *Ambystoma jeffersonianum* (GREEN, 1827), *Ambystoma texanum* (MATTHES, 1855) and *Ambystoma laterale* (HALLOWELL, 1857), and several all-female "forms" issued from the hybridization of these species. Two of these forms are known as *Ambystoma platineum* (COPE, 1867) and *Ambystoma tremblayi* COMEAU, 1943. The situation here is quite similar to that of the triploid gyno-

genetic forms of *Poeciliopsis* mentioned above (see review in UZZELL and GOLDBLATT 1967, and see also UZZELL 1970; WILBUR 1971; CUELLAR 1976; DOWNS 1978, etc.). *A. platineum* possesses 2 sets of chromosomes from *A. jeffersonianum* and one from *A. laterale*, while *A. tremblayi* possesses 2 sets from *A. laterale* and one from *A. jeffersonianum*. Possibly these forms arose also through 2 successive hybridizations: first a simple hybridization between *A. jeffersonianum* and *A. laterale*, then hybridization between hybrid females producing unreduced diploid eggs and males of the parental species, respectively *A. jeffersonianum* to produce *A. platineum*, and *A. laterale* to produce *A. tremblayi*. As in the case of the gynogenetic *Poeciliopsis*, these triploid females produce unreduced triploid gametes which are activated in nature by sperm from the "parental" species, respectively *A. jeffersonianum* for *A. platineum* and *A. laterale* for *A. tremblayi*. Recently, DOWNS (1978) described a more complicated situation, involving both diploid and triploid all-female specimens issued from hybridization between *A. laterale* and *A. texanum*. However, he did not ascertain the exact mode of reproduction of these forms, which may be gynogenetic, hybridogenetic or even parthenogenetic.

1.3. Hybridogenetic frogs

The evolutionary situation observed in European green-frogs or water-frogs (Anura, Ranidae) is even more complicated than in the foregoing cases. This group has been the matter of numerous works during the last 15 years (see review up to 1976 in DUBOIS 1977; and see also GRAF, KARCH and MOREILLON 1977; UZZELL, GÜNTHER and BERGER 1977; GRAF and MÜLLER 1979; GÜNTHER et al. 1979; TUNNER 1980, etc.).

European green-frogs include several "good" species, among which *Rana lessonae* CAMERANO, 1882, *Rana ridibunda* PALLAS, 1771, *Rana perezi* SEOANE, 1885 and probably several other still unnamed species, one of which has recently been called "Southern non-hybrid" by UZZELL and HOTZ (1979). Beside these species, the group also includes several "forms" of hybrid origin and with a particular mode of reproduction. The best studied of these forms is the frog known as *Rana esculenta* LINNAEUS, 1758, which originated by hybridization between *Rana lessonae* and *Rana ridibunda*. A second hybrid form, recently discovered, possesses one set of chromosomes from *Rana ridibunda* and one from *Rana perezi* (GRAF, KARCH and MOREILLON 1977). A third hybrid form was even more recently described by UZZELL and HOTZ (1979) who called it "Southern hybrid": it possesses one set of chromosomes from *Rana ridibunda* and one from the "Southern non-hybrid" species. Since only the first of these 3 hybrid forms has been the matter of numerous and detailed studies, the discussion below will be focused on it.

In contrast to the above mentioned hybrid forms of fish and salamanders, *Rana esculenta* is not, as a rule, a unisexual form: both sexes are observed in most populations, although sometimes with different frequencies. On the other hand, several types of populations of these frogs exist: *Rana esculenta* may live in sympatry with *Rana lessonae* or with *Rana ridibunda*, and is even able to form "pure" *Rana esculenta* populations. According to the frequencies of the different phenotypes within the populations, GÜNTHER (1975) designated these as *esculenta* populations (e-P), *esculenta-lessonae*

populations (*e-l-P*), *lessonae-esculenta* populations (*l-e-P*), *esculenta-ridibunda* populations (*e-r-P*), and *ridibunda-esculenta* ♂♂ populations (*r-e♂-P*). Another complication comes from the fact that in some of these populations *R. esculenta* frogs are all diploid, while in others part of these frogs are diploid and part of them triploid.

In mixed populations, matings between *R. esculenta* and *R. lessonae* or between *R. esculenta* and *R. ridibunda* are frequent. The offspring from such crosses show no intermediate character and have "pure" *R. esculenta* phenotypes and genotypes. In all kinds of populations, it seems that *R. esculenta* frogs produce only 3 kinds of functional gametes, containing either a complete chromosome set from *R. ridibunda*, a complete set from *R. lessonae* and/or diploid gametes that contain complete genomes from both parental species. Recombination between *lessonae* and *ridibunda* genomes is not totally absent, but is extremely restricted. In *l-e-P*, *R. esculenta* frogs during their meiosis eliminate mainly the *lessonae* genome and form almost exclusively pure *ridibunda* gametes. The *R. esculenta* phenotypes of these populations are therefore mainly obtained from crosses between *R. esculenta* and *R. lessonae*. In *r-e♂-P*, the *R. esculenta* males mainly produce *lessonae* gametes that contain a male determining factor: these males reproduce with *R. ridibunda* females and the offspring from such crosses consists again only of *R. esculenta* males. Finally, in the populations where *R. esculenta* specimens occur alone (*e-P*) or where they are numerically predominant (*e-l-P* and *e-r-P*), *R. esculenta* phenotypes originate only or mainly from matings between males and females *R. esculenta*. In such populations, both diploid and triploid *R. esculenta* specimens occur. In these individuals, recombinations between the *lessonae* and the *ridibunda* genomes are very limited, and therefore these frogs produce "pure" *lessonae* or *ridibunda* gametes. Mating between two *R. esculenta* frogs producing *ridibunda* gametes, or between two *R. esculenta* frogs producing *lessonae* gametes are generally sterile or give birth to offspring having a *R. ridibunda* or a *R. lessonae* phenotype, but usually with a greatly reduced vitality. In such populations, the most successful crosses are those between *R. esculenta* specimens in which one partner produces *lessonae* and the other *ridibunda* gametes. Such crosses result in "pure" *R. esculenta* frogs.

TUNNER (1974) was the first to point to the similarity of the genetic phenomena observed in green-frogs and those described earlier in *Poeciliopsis* under the name hybridogenesis, and suggested that *Rana esculenta* was also a hybridogenetic form. Other recent studies have confirmed this opinion in certain cases (GRAF and MÜLLER 1979). However, in studies dealing with other populations, the hybridogenetic mechanism in the meiosis of *Rana esculenta* was shown to be imperfect, and for such situations the formula "leaky hybridogenetic system" was suggested (see UZZELL, GÜNTHER and BERGER 1977).

2. Klepton and synklepton

Many authors until now have dealt with forms such as *Poecilia formosa*, *Ambystoma platineum* or *Rana esculenta* as if they were "biological" species. However the data summarized above concerning the reproductive patterns of these forms clearly show

that these do not fit the "biological species concept" as defined by MAYR (1942, 1963) and others, and as now accepted by most of the evolutionary biologists (see e.g. the recent survey of the "species problem" in BOCQUET, GÉERMONT and LAMOTTE 1976, 1977, 1980).

Forms such as hybridogenetic and gynogenetic *Poeciliopsis* gynogenetic *Poecilia* and *Ambystoma*, hybridogenetic or leaky hybridogenetic *Rana* and other similar cases, although they all have specific particularities which make each of them a unique case, have several features in common:

(1) All these forms are of hybrid origin. Some of them arose by hybridization between 2 "good" species, and others by hybridization between a "good" species and a hybrid form.

(2) These forms do not behave genetically as "good" species but have rather genetic characteristics of clones. Hybridogenetic and leaky hybridogenetic forms are hemi-clones; gynogenetic forms are full clones.

(3) Such forms cannot survive alone in nature. They require the gametes of other species for their own reproduction, thus realizing a kind of "sexual parasitism".

The first two features listed above may also be found in other "forms" than those considered in this paper. Thus, a hybrid origin has also been demonstrated or postulated both for some "good" species (see in particular the case of the polyploid species of Anurans, reviewed and discussed by DUBOIS 1977 and BOGART 1980) and for certain "parthenogenetic forms", also called by WHITE (1978) "thelytokous species" or "biotypes" (see in particular the case of the "unisexual species" of lizards, reviewed and discussed by COLE 1975; WHITE 1978; see also CUELLAR 1977; Vanzolini, WRIGHT, COLE and CUELLAR 1978). In the polyploid species of Anurans mentioned above, breeding and gene flow between individuals take place as in "normal" species, and it would be irrelevant to create a special category for these species merely on account of their polyploidy. On the other hand, "thelytokous biotypes" do not have genetic characteristics of species, but of clones, as have the particular forms studied in this paper. They differ from the latter, however, in that they do not depend for their reproduction on another form or species.

Actually, despite the great diversity of individual "atypical" biological situations which have been described (see e.g. the review of "asexual speciation" in WHITE 1978), it seems possible to group all existing situations (including "normal" ones) within three major categories, which do not seem to have been recognized as such by authors who have discussed the taxonomic problems related with these "atypical" forms (see e.g. MASLIN 1968 and references therein):

(1) "Biological" species, with biparental sexual reproduction, including free breeding between members of the species, recombination between parental genomes during meiosis, etc. Species reproduce and evolve independently from one another.

(2) Uniparental forms with clonal heredity. Reproduction in such forms may be truly asexual (e.g. asexual multiplication of certain Protozoa), or sexual or parasexual (e.g. autofertilization, thelytoky). In the latter case, the "atypical" mode of reproduction

is clearly derived from normal biparental sexual reproduction. Such forms have lost some of the characteristics of "biological" species (intrabreeding, recombination, etc.), but they share with 'them' the feature of reproducing and evolving independently from one another.

(3) Gynogenetic and hybridogenetic forms, as described above. They have a para-sexual mode of reproduction, clearly derived from normal sexual reproduction. They may be unisexual or bisexual. At each generation, they need a gametic contribution from other species or forms in order to achieve their reproduction, and are therefore dependent on these forms for their perpetuation. Heredity in such forms is fully clonal or hemiclonal.

We are convinced that both categories (2) and (3) are distinct from each other and from (1), and should require different designations and nomenclatural treatments. In this paper, however, we will limit our discussion to the forms belonging to the category (3).

Forms having such characteristics cannot be considered as "biological" species. On the other hand, such situations are not accounted for by any of the existing categories of evolutionary systematics, such as superspecies and prospecies, ultraspecies and dualspecies, etc. (for a review of these categories at the specific and infrageneric supraspecific level, see BERNARDI 1980). We therefore propose to coin a new word to accommodate these forms, and we suggest the word klepton (plural: kleptons; adjective: kleptic), derived from the Greek *Kλέπτης* (thief), which refers to the fact that such forms are "stealing" gametes from other species to realize their reproduction.

Two different kinds of kleptons may be distinguished: gynogenetic and hybridogenetic ones. This distinction is however of secondary importance in contrast with the fact that all kleptons share the common characteristics listed above, and should in our opinion not be overstressed by the creation of two different names for these two categories.

Apart from one exception which will be discussed below, in all known cases a given klepton never lives alone, but in sympatry with one or both of the "good" species from which it arose by hybridization. The group consisting of both parental species and of the klepton has an evolutionary meaning and a reality in nature. Furthermore, in several known cases this group is even larger, including more than two "good" species and more than one klepton. We suggest to call synklepton such a group which consists of two or more species and of one or more kleptons issued from the hybridization of these species.

It should again be stressed that, in our mind, a klepton is not a species. Neither is it a subspecies, nor can it simply be considered as a hybrid population. Kleptons are not "normal" F1 hybrids produced by recent crossings between parental species, but may have been maintained as such for thousands of years (see BÖHME and GÜNTHER 1979). Furthermore, in several cases it appears most likely that a new klepton may arise by new hybridization between an existing klepton and another klepton or a "good" species, which may be either one of the two parental species of the former, or a third one. Such multihybrid origins have been suggested for several kleptons of the

genera *Poeciliopsis* and *Ambystoma*. In green-frogs, the klepton recently discovered in Southern France, which has one set of chromosomes from *Rana ridibunda* and one from *Rana perezi*, might well have arisen through hybridization of the species *Rana perezi*, present in Southern France, with the klepton *Rana esculenta*, present in Central France, *Rana ridibunda* being totally absent from both these regions.

In general, kleptons cannot reproduce without the help of gametes "stolen" from a distinct species. A particular situation is however met with in the case of *Rana esculenta*: while in most mixed populations (either with *R. lessonae* or *R. ridibunda*) this form behaves as a "normal" klepton, in pure *R. esculenta* populations or in populations where *R. esculenta* is largely predominant, this form is able to reproduce by itself and could appear at first examination to have reached in such cases the status of a "good" species. Although this might be formally accepted as true, the meiosis of individuals from these populations prove to be abnormal, without recombination between *lessonae* and *ridibunda* genomes, and these individuals produce almost only "pure" *lessonae* or *ridibunda* gametes, as in mixed populations. In such populations, every individual of *R. esculenta* may be considered to play both the role of a klepton and that of a "good" species in any given cross. We suggest to consider that in this case, where both meiosis and gene flow are abnormal as compared with "true" species, the status of a "biological" species has not been reached, and that individuals of such populations should still be considered as members of the klepton *Rana esculenta*.

A given klepton may thus be a rather heterogeneous assemblage of several types of individuals or of different populations having slightly different genetic and other characteristics. This does not prevent kleptons from having a real unity.

In particular, within a given klepton several distinct clones or hemiclones issued from independent hybridization events or from other sources of variation subsequent to the initial hybridization may coexist (see e.g. UZZELL and GOLDBLATT 1967; TUNNER 1974; UZZELL and BERGER 1975; TUNNER and DOBROWSKY 1976; VRIJENHOEK 1978; VRIJENHOEK, ANGUS and SCHUTZ 1978; ANGUS and SCHULTZ 1979; MOORE and EISENBREY 1979, etc.). The possibility could indeed be contemplated to consider formally each of these clones as a distinct klepton, but such a practice would not do justice to the fact that all these clones are essentially similar in their origin, genetic constitution, phenetic and ecological characteristics, and may in general be sympatric. All members of a given klepton have the same "macro" origin and genetic constitution, since they possess two (or more) genomes from the same two (or more) parental species. However in kleptons consisting of several clones (or hemiclones) appeared through independent hybridization events, these different clones have different "micro" origins and genetic constitutions. When these clones are sympatric, it seems irrelevant to distinguish them taxonomically. Possibly however, when such clones having slightly different genetic characteristics have allopatric or parapatric distributions, it might be useful to acknowledge their differences by recognizing the existence of two or more distinct subkleptons within a single klepton, just as subspecies may be distinguished within a species. For a further discussion of this aspect, MASLIN's (1968) interesting discussion of "uniparental subspecies" may be consulted.

Morphologically, all members of a given klepton are usually very similar, at least as similar between them as are members of a "biological" species. They also usually have similar ecological characteristics, which make the klepton a significant unit for ecological studies. Kleptons are therefore genuine genetic, phenetic and ecological units, and qualify as natural taxa, as well as do bisexual species or subspecies, although in a different way. This is clearly outlined by the fact that several kleptons have long been treated as "normal" species: such is the case of *Rana esculenta*, which was named by LINNAEUS in 1758 and considered a valid species until very recently, despite the very high number of studies of all kinds which have dealt with this "form".

Kleptons may thus best be viewed as groups of animals of common or similar hybrid origin which share certain genetic, phenetic and ecological characteristics, but which do not have between them the genetic relationships that exist between members of "biological" species (free intrabreeding, with recombination of parental genes during meiosis at each generation, etc.) and which depend for their reproduction on gametes produced by animals belonging to distinct species or kleptons.

3. Nomenclatural problems

Several authors have discussed the problems associated with the nomenclature of "atypical" forms such as kleptons, "parthenogenetic forms", etc. (see e.g. WRIGHT and LOWE 1967; MASLIN 1968; SCHULTZ 1969, 1977; GÉNERMONT 1980, etc.). Since most of these forms are of hybrid origin, some of these authors have suggested to coin special names indicating this origin, while others have used simple names unrelated to those of the parental species. At present, no general rule exists concerning the nomenclature of kleptons.

Four different kinds of nomenclatures have been used or suggested by the authors for these forms. As will be shown below, each of these methods has its drawbacks:

(1) Rather numerous authors have continued to use "normal" names for kleptons, as in the case of "biological" species, even after these forms have been shown to have "atypical" genetic characteristics. This is the case in particular of most of the authors who have dealt with green-frogs, even in recent years, who simply used the name *Rana esculenta* without any special mark indicating that this form is not a "true" species. Similar "normal" names were also used by authors dealing with kleptic fish (*Poecilia formosa*) or salamanders (*Ambystoma platineum*, *Ambystoma tremblayi*). Such names are not advisable for kleptons, because they give the wrong impression that they designate "biological" species.

(2) Some authors suggested to indicate the fact that kleptons are not "normal" species by placing their "specific" names between quotation marks. Thus, HUBBS and HUBBS (1932), when they discovered the first case of kleptic fish, used for it the denomination *Mollienisia "formosa"*, but, as mentioned above, subsequent authors have come back to a more "classical" writing and this form is now known simply as *Poecilia formosa*. In green-frogs, GÜNTHER (1973) first proposed the notation "*Rana esculenta*", but later (GÜNTHER and HÄHNEL 1976) corrected it into *Rana "esculenta"*,

since it is clear that this form belongs to the genus *Rana*; a few other authors (e.g. DUBOIS 1977, 1979; KOREF-SANTIBÁÑEZ 1979; BOGART 1980) also adopted the notation *Rana "esculenta"*, but here also a majority of authors retained the traditional denomination *Rana esculenta* (see e.g. the various contributions in GÜNTHER et al. 1979). As a matter of fact, a notation using quotation marks for kleptons is not very advisable, because it is equivocal. A similar notation may also be employed to designate specimens the exact determination of which is not certain, or to draw the attention to the existence of a nomenclatural problem. For example DUBOIS (1977), followed by BOGART (1980), used a similar notation in the case of diploid-polyplid pairs of dualspecies for which a single name had been used by previous authors, in order to show that this single name was in fact applied to two distinct "biological" species.

(3) To designate unisexual forms of the genus *Poeciliopsis*, SCHULTZ (1961, 1966, 1967) first used denominations such as *Poeciliopsis Cx* and *Poeciliopsis Fx*, or, more shortly, *Cx*, *Cy* and *Cz*. Such symbols have the clear advantage of not being mistakable for names of "biological" species, but the disadvantage of not being true names.

(4) SCHULTZ himself appears to have recognized this latter disadvantage, and in 1969 proposed a new system of nomenclature for these forms, "for those who prefer to have names for animals rather than symbols" (SCHULTZ 1969: 608). In this system, kleptons receive compound names that indicate their basic genotype. Thus the diploid klepton which possesses one genome from *Poeciliopsis monacha* and one from *Poeciliopsis lucida* was named *Poeciliopsis monacha-lucida* and the triploid klepton which possesses two genomes from *Poeciliopsis monacha* and one from *Poeciliopsis lucida* was named *Poeciliopsis 2 monacha-lucida*. In the case of some kleptons which could be shown to be of trihybrid origin (VRIJENHOEK and SCHULTZ 1974; SCHULTZ 1977), multicompound names such as *Poeciliopsis monacha (viriosa)-lucida* have been coined (SCHULTZ 1977). SCHULTZ (1977) and GÉNERMONT (1980) suggested to generalize this mode of nomenclature to all forms of hybrid origin. We do not support this proposal, for several reasons:

(a) Although they have the advantage of clearly indicating the origin of kleptons, such compound names are highly unpalatable, especially in the cases where more than two initial genomes are present in the genotype of the klepton.

(b) Such names cannot be employed in the case where a single klepton includes specimens with different chromosome numbers. Thus, the populations of *Rana esculenta* may consist of only diploid individuals (with one *lessonae* and one *ridibunda* genome), but they may also include more or less numerous triploid specimens (with two *lessonae* and one *ridibunda*, or two *ridibunda* and one *lessonae* genomes), which may also take part in the reproduction and in the maintenance of such populations (see GÜNTHER, UZZELL and BERGER 1979). Following SCHULTZ' proposal would require giving three different names (*Rana lessonae-ridibunda*, *Rana 2 lessonae-ridibunda*, *Rana lessonae-2 ridibunda*) to these three different kinds of frogs, which would not only complicate the nomenclature of these frogs, but also obscure the fact that these three different kinds of frogs are members of a single genetic system and should be included in a single klepton.

(c) If kleptons, as we submit, are to be considered as valid taxa, they should be designated by unique names, as are other taxa such as species or subspecies. It seems to us irrelevant to indicate in the name of these taxa their hypothesized or demonstrated origin: specific names of species are not based on the names of their supposed or known ancestral species. Unique, simple names are particularly necessary for kleptons which are to be used or mentioned in biological research works of various kinds (ecology, physiology, biochemistry, etc.).

(d) Finally, and perhaps most importantly, SCHULTZ's proposal would entail rather important nomenclatural changes in some groups. Various kleptons, such as *Poecilia formosa*, *Ambystoma platineum* or *Rana esculenta*, were first believed to be valid species, and were described and named as such. These names have sometimes been in very general use for long periods of time, and it would be most irrelevant, when the proper evolutionary status and the genetic features of these taxa are discovered, to change their names merely in order to indicate their origin and genetic constitution, especially in all cases where the taxon in itself remains unchanged as far as its limits and included individuals are concerned. It seems quite likely that in the future additional taxa currently considered to be species or subspecies will be shown to be kleptons. For the sake of the stability of nomenclature, a conservative attitude towards existing names is to be commended: these names should be retained, but transferred from the category species (or subspecies) to the category klepton. Such an operation is similar to the one realized when, for example, a form described as a subspecies is raised to the species rank, or the reverse.

It is our opinion that, at the stage now reached by studies dealing with gynogenetic and hybridogenetic forms, a general and unique system of nomenclature should be adopted for all of them.

Although, as discussed above, kleptons are not species, they are not artificial units: they correspond to real genetic, phenetic and ecological units. In our opinion, the category klepton could be best treated as a third category of the species-group, distinct from both the categories species and subspecies. We believe that any system of nomenclature of taxa of this category should meet with the following requirements:

(1) Names of kleptons should be written in a special way, in order to make it clear, by simple reading, that they apply to kleptons and not to species or subspecies.

(2) Such names should be Latin names, formed in concordance with the provisions of the International Code of Zoological Nomenclature for names of the species-group, and should follow the same nomenclatural Rules as these names. Therefore, the name of a klepton should be composed of a single word and should always be used in combination with a genus-group name. To become available, such a name should first be published accompanied by a description, definition or indication. Names of kleptons should follow the Law of Priority and the Law of Homonymy.

(3) Kleptons, as other taxa of the species-group, should be based on type-specimens (holotypes, syntypes, lectotypes or neotypes).

(4) It is too early in our opinion to know whether the category subklepton, as shortly discussed above, will prove useful and will be adopted by evolutionary biologists inter-

ested in kleptons. If it was, the subkleptic name should appear as a third word after the generic and kleptic names, and should follow the same nomenclatural Rules as subspecific names of polytypic species.

If these conditions are accepted, it is clear that a new nomenclatural system must be devised for kleptons, since none of the four systems now in use and described above meets with these requirements.

The condition (1) prompts us to propose a new mode of notation to distinguish names of kleptons from names of species and subspecies. We suggest to place the abbreviation "kl." between the genus-group name and the species-group name of kleptons. We have also considered the possibility to place this abbreviation before the generic name, in order to follow in a certain way BRADLEY's (1957: 114) proposal (not included, however, in the subsequent editions of the Code) to provide hybrids of which one parent is not known with names of the form " \times *Coregonus dulosus Fatio*". However the evolutionary status of kleptons is "abnormal" only at the specific level but not, at least in all cases presently known, at the generic level: all known kleptons clearly belong to a given genus, which is the same as that of the "good" species from which they originated. Therefore it seems better to include the sign "kl." between the generic and kleptic names. In our opinion the inclusion of this mark in the names of kleptons should be obligatory and not optional, in order to avoid possible confusions with the names of species. In the case where a subkleptic name would have to be added, it should simply follow the kleptic name without any additional mark.

In order to follow the requirement (2) above, all known kleptons should be called by a single name, and according to the Law of Priority this name should be the first one proposed for this klepton, although in some cases the spelling of this name should be emended in order to follow the Rules. In many cases, this Rule would greatly simplify nomenclatural problems. Names first given to what was first believed to be a species, such as *Poecilia formosa* (GIRARD, 1859), *Ambystoma platineum* (COPE, 1867) or *Rana esculenta* LINNAEUS, 1758, could be automatically transferred, when necessary, to the corresponding kleptons, provided the sign "kl." is added between the generic and kleptic names. On the other hand, names such as *Poeciliopsis monacha-lucida*, *Poeciliopsis 2 monacha-lucida* or *Poeciliopsis monacha-2 lucida* should be emended following the Articles 26 and 32 of the Code. The corresponding kleptons should be called respectively *Poeciliopsis kl. monachalucida* SCHULTZ, 1969, *Poeciliopsis kl. duomonachalucida* SCHULTZ, 1969 and *Poeciliopsis kl. monachaduolucida* SCHULTZ, 1969. Finally, for kleptons that have been described but still not named, new names should be coined. We suggest that such new names should be short, simple words, as in the case of normal specific or subspecific names, and not long, unpalatable compound names. All kleptic names would have a status in nomenclature, and would compete with specific and subspecific names as far as the Laws of Priority and of Homonymy are concerned. Such a Rule appears most advisable in order to avoid possible nomenclatural confusions.

Finally we suggest that a provision should be made for the possibility of including the name of the synklepton in the scientific names of both "good" species and kleptons which belong to it. For this it must be stressed that, following a suggestion of BERNARDI

Table 1. Nomenclature suggested for some species and kleptons belonging to four synkleptons of fish, salamanders and frogs

Current names	Suggested names	
	Abbreviated names	Complete names
<i>Poeciliopsis latidens</i>	<i>Poeciliopsis latidens</i>	<i>Poeciliopsis</i> (synkl. <i>occidentalis</i>) <i>latidens</i> (GARMAN, 1895)
<i>Poeciliopsis lucida</i>	<i>Poeciliopsis lucida</i>	<i>Poeciliopsis</i> (synkl. <i>occidentalis</i>) <i>lucida</i> MILLER, 1960
<i>Poeciliopsis monacha</i>	<i>Poeciliopsis monacha</i>	<i>Poeciliopsis</i> (synkl. <i>occidentalis</i>) <i>monacha</i> MILLER, 1960
<i>Poeciliopsis occidentalis</i>	<i>Poeciliopsis occidentalis</i>	<i>Poeciliopsis</i> (synkl. <i>occidentalis</i>) <i>occidentalis</i> (BAIRD and GIRARD, 1853)
<i>Poeciliopsis</i>	<i>Poeciliopsis</i> kl.	<i>Poeciliopsis</i> (synkl. <i>occidentalis</i>)
2 <i>monacha-lucida</i>	<i>duomonachalucida</i>	kl. <i>duomonachalucida</i> SCHULTZ, 1969
<i>Poeciliopsis</i>	<i>Poeciliopsis</i> kl.	<i>Poeciliopsis</i> (synkl. <i>occidentalis</i>)
<i>monacha-2 lucida</i>	<i>monachaduolucida</i>	kl. <i>monachaduolucida</i> SCHULTZ, 1969
<i>Poeciliopsis</i>	<i>Poeciliopsis</i> kl.	<i>Poeciliopsis</i> (synkl. <i>occidentalis</i>)
<i>monacha-latidens</i>	<i>monachalatidens</i>	kl. <i>monachalatidens</i> SCHULTZ, 1971
<i>Poeciliopsis</i>	<i>Poeciliopsis</i> kl.	<i>Poeciliopsis</i> (synkl. <i>occidentalis</i>)
<i>monacha-lucida</i>	<i>monachalucida</i>	kl. <i>monachalucida</i> SCHULTZ, 1969
<i>Poeciliopsis</i>	<i>Poeciliopsis</i> kl.	<i>Poeciliopsis</i> (synkl. <i>occidentalis</i>)
<i>monacha-occidentalis</i>	<i>monachaoccidentalis</i>	kl. <i>monachaoccidentalis</i> SCHULTZ, 1971
<i>Poecilia latipinna</i>	<i>Poecilia latipinna</i>	<i>Poecilia</i> (synkl. <i>latipinna</i>) <i>latipinna</i> (LESUEUR, 1821)
<i>Poecilia mexicana</i>	<i>Poecilia mexicana</i>	<i>Poecilia</i> (synkl. <i>latipinna</i>) <i>mexicana</i> STEINDACHNER, 1863
<i>Poecilia formosa</i>	<i>Poecilia</i> kl. <i>formosa</i>	<i>Poecilia</i> (synkl. <i>latipinna</i>) kl. <i>formosa</i> (GIRARD, 1859)
<i>Ambystoma jeffersonianum</i>	<i>Ambystoma jeffersonianum</i>	<i>Ambystoma</i> (synkl. <i>jeffersonianum</i>) <i>jeffersonianum</i> (GREEN, 1827)
<i>Ambystoma laterale</i>	<i>Ambystoma laterale</i>	<i>Ambystoma</i> (synkl. <i>jeffersonianum</i>) <i>laterale</i> (HALLOWELL, 1857)
<i>Ambystoma platineum</i>	<i>Ambystoma</i> kl. <i>platineum</i>	<i>Ambystoma</i> (synkl. <i>jeffersonianum</i>) kl. <i>platineum</i> (COPE, 1867)
<i>Ambystoma tremblayi</i>	<i>Ambystoma</i> kl. <i>tremblayi</i>	<i>Ambystoma</i> (synkl. <i>jeffersonianum</i>) kl. <i>tremblayi</i> COMEAU, 1943
<i>Rana lessonae</i>	<i>Rana lessonae</i>	<i>Rana</i> (synkl. <i>esculenta</i>) <i>lessonae</i> CAMERANO, 1882
<i>Rana perezi</i> or <i>Rana ridibunda perezi</i>	<i>Rana perezi</i>	<i>Rana</i> (synkl. <i>esculenta</i>) <i>perezi</i> SEOANE, 1885
<i>Rana ridibunda</i>	<i>Rana ridibunda</i>	<i>Rana</i> (synkl. <i>esculenta</i>) <i>ridibunda</i> PALLAS, 1771
<i>Rana esculenta</i> or <i>Rana „esculenta“</i>	<i>Rana</i> kl. <i>esculenta</i>	<i>Rana</i> (synkl. <i>esculenta</i>) kl. <i>esculenta</i> LINNAEUS, 1758

and MELVILLE (1979), the International Commission on Zoological Nomenclature recently included in the Article 6 of the new edition of the Code, which is now in preparation, a new Rule which provides for the possibility of interpolating a species-group name in parenthesis between the genus-group name and the species-group name, to represent a supraspecific infrasubgeneric taxon such as a superspecies (for more details, see BERNARDI 1980). We suggest to follow this new Rule and to admit the possibility of including, when deemed necessary, the synkleptic name between the generic and the specific or the kleptic name. For naming the synklepton we will also follow the new Code in preparation, which states in its Article 23 that the valid name for such a supraspecific taxon is the oldest valid name of those of the included taxa of the species-group. Thus in the case of *Poeciliopsis* the synklepton should bear the name of *occidentalis* BAIRD and GIRARD, 1853, in the case of *Poecilia* the name of *latipinna* LESUEUR, 1821, in the case of *Ambystoma* the name of *jeffersonianum* GREEN, 1827 and in the case of *Rana* the name of *esculenta* LINNAEUS, 1758.

In Table 1 we have given a partial list of species and kleptons included in the 4 synkleptons discussed in the text. For each of these taxa we give the current name and the name suggested on the basis of the present discussion. This latter name may be presented either in a complete form (including the name of the synklepton and of the author of the species-group name) or in an abbreviated one, which is more likely to be used in most works dealing with these animals.

4. Conclusion

In this paper we have pointed to the existence, beside "true biological species", of two other kinds of animal "forms": uniparental forms with clonal heredity, which are not discussed further here; and hybridogenetic and gynogenetic forms, which are the matter of this work. Such forms, for which we propose the new name klepton, were recently discovered and studied in the genera *Poeciliopsis*, *Poecilia*, *Ambystoma* and *Rana*. They are of hybrid origin, have particular genetic characteristics (with clonal or hemicalonal heredity), and require the gametes of other species for their own reproduction.

Kleptons need not be "evolutionary dead-ends". They may constitute intermediate steps leading to other forms, such as polyplloid bisexual "good" species (see e.g. the discussions in DUBOIS 1977 and BOGART 1980). This does not prevent biologists however from the necessity of giving them special names, in order to point to their evolutionary and genetic particularities. The same applies to other special evolutionary situations such as those for which categories such as superspecies, pro-species, and related ones were created (see BERNARDI 1980).

We hope the suggestions made here will help to homogenize and stabilize the nomenclature of kleptons in all animal groups and will therefore draw the attention of biologists, who may meet with such names in faunistic or ecological lists, etc., to the special problems associated with the evolutionary biology of these forms.

Résumé

Les travaux récents ont mis en évidence l'existence dans la nature de "formes" animales particulières qui ne peuvent pas être considérées comme de "vraies espèces", telles que les formes unisexuées, gynogénétiques et hybridogénétiques, de poissons des genres *Poeciliopsis* et *Poecilia*, les formes unisexuées gynogénétiques d'Urodèles du genre *Ambystoma*, et les formes hybridogénétiques d'Anoures du genre *Rana*. Toutes ces formes, malgré leur diversité, ont les caractéristiques suivantes

en commun: elles sont d'origine hybride; leur hérédité est de mode clonal ou hémiclonal; pour leur reproduction, ces formes ont besoin de faire appel aux gamètes d'une autre "bonne espèce". Nous proposons de désigner ces formes du nom de kleptons, et d'appeler synkleptons les groupes consistant en deux "bonnes espèces" (ou plus) et d'un klepton (ou de plusieurs) issu(s) de l'hybridation de ces espèces. Nous proposons de considérer les kleptons comme des taxons du groupe-espèce, appartenant à une troisième catégorie taxinomique distincte de celles d'espèce et de seu-espèce. Les noms kleptiques devraient donc être soumis aux mêmes Règles nomenclaturales que les noms spéciifiques ou subspécifiques. Nous proposons un mode uniforme de notation pour les kleptons et synkleptons. Les kleptons devraient porter des noms du type *Rana* (synkl. *esculenta*) kl. *esculenta* LINNÉ, 1758, ou, plus brièvement, *Rana* kl. *esculenta*. Quant aux "bonnes espèces" appartenant aux mêmes synkleptons, elles devraient être désignées par des noms du type *Rana* (synkl. *esculenta*) *lessonae* CAMERANO, 1882, ou, plus brièvement, *Rana lessonae*.

Zusammenfassung

Das Ziel des Artikels ist es, einen allgemeinen Begriff zu prägen sowie Nomenklaturregeln zu unterbreiten für einige besondere „Formen“ von Tieren, die, wie die gynogenetischen und hybridogenetischen unisexuellen Fische der Gattung *Poeciliopsis*, die gynogenetischen unisexuellen Fische der Gattung *Poecilia*, die gynogenetischen unisexuellen Salamander der Gattung *Ambystoma* und die hybridogenetischen (oder defekt hybridogenetischen) Frösche der Gattung *Rana*, nicht als „biologische“ Arten angesehen werden können. Alle diese Formen haben trotz bestehender Unterschiede folgende gemeinsame Merkmale: Sie sind hybriden Ursprungs; ihre Vererbung ist klonal oder hemiclonal; zu ihrer Fortpflanzung benötigen sie die Gameten einer anderen Spezies.

Wir schlagen vor, solche Formen als „Klepton“ zu bezeichnen und wählen für eine Gruppe, die sich aus zwei oder mehr „guten“ Arten und einem oder mehreren Kleptons — hervorgegangen aus der Bastardierung dieser Arten — zusammensetzt, den Ausdruck „Synklepton“. Das Klepton ist unserer Meinung nach eine besondere taxonomische Kategorie der Art-Gruppe und infolgedessen abzugrenzen von den Kategorien Spezies und Subspezies. Die Namen von Kleptons sollten den gleichen Nomenklaturregeln unterliegen wie die von Arten und Unterarten.

Wir fordern, alle Kleptons und Synkleptons in gleicher Weise zu bezeichnen. So sollte beispielsweise der Teichfrosch den Namen *Rana* (synkl. *esculenta*) kl. *esculenta* LINNAEUS, 1758 oder in der Kurzform *Rana* kl. *esculenta* erhalten, während z. B. eine der „guten“ Arten, welche zum gleichen Synklepton gehört, als *Rana* (synkl. *esculenta*) *lessonae* CAMERANO, 1882 oder in der Kurzform, als *Rana lessonae* zu bezeichnen wäre.

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