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Brachyuran systematics and the position of the family Raninidae reconsidered

Систематика брахиур и новый взгляд на положение семейства Raninidae

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КЛЮЧЕВЫЕ СЛОВА: Brachyura, Dromiacea, Raninidae, однородность, положение в системе.

ABSTRACT: A discussion concerning the hierarchical system of the brachyuran crabs (Crustacea Decapoda Brachyura) has been recently renewed by many carcinologists. Besides the classical method based on homologies, some new methods used in brachyuran systematics have revealed new questions as regards the brachyuran classification. Accordingly, the homogeneity of the Brachyura, the systematic position of the family Raninidae, and the homogeneity of the family Dromiidae are reconsidered. Based on an analysis of all available data, the present state of knowledge is concluded to provide no sufficient evidence to reject the classical brachyuran classification. Thus, the Dromiacea is part of the Brachyura, the Raninidae belongs to the Dromiacea, and the Dromiidae is a homogeneous family.

РЕЗЮМЕ: В последнее время среди карцинологов с новой силой возобновилось обсуждение иерархической системы крабов (Crustacea Decapoda Brachyura). Новые методы, используемые в систематике крабов наряду с классическими, основанными на гомологиях, привели к постановке ряда новых проблем классификации этой группы. В соответствии с этим, заново обсуждается однородность Brachyura, положение в системе семейства Raninidae и однородность семейства Dromiidae. В результате анализа всех имеющихся данных сделано заключение, что в настоящее время нет оснований отвергать классическую классификацию Brachyura. Таким образом, Dromiacea являются частью Brachyura, Raninidae относятся к Dromiacea, a Dromiidae сами по себе являются однородным семейством.

Introduction

Discussions concerning the classification of the higher brachyuran taxa, such as the homogeneity of the Brachyura and Dromiacea and, in particular, the systematic position of the family Raninidae are "eternal" themes attracting the attention of many carcinologists. Numerous modern authors such as Sakai [1976]; Guinot [1978]; de Saint Laurent [1980a, 1980b]; Rice [1980, 1981a, 1981b]; Manning & Holthuis [1981]; Bowman & Abele [1982]; Williams [1984]; Schram [1986]; Dai & Yang [1991] have considered directly or indirectly some principal problems of brachyuran classification based on adults and larvae. Recently, Jamieson [1989, 1991, 1993] and Jamieson & Tudge [1990] presented data on the ultrastructure of the spermatozoa which are relevant to the the classification of crabs. Quite recently, Spears et al. [1992] once again questioned the systematic problems of the brachyuran crabs. Since the papers by Jamieson and Spears et al. concern some outstanding problems of brachyuran systematics and because I have been involved in these studies [Stevčić, 1971, 1973], I have been inspired to join this discussion and reconsider some pertinent problems. Consequently, the topic of the present paper is a re-examination of some pertinent problems of higher brachyuran taxa in the light of old and new findings.

Spears et al. [1992: 447] addressed three principal questions: "(1) whether the Brachyura as currently defined (i.e., including the Dromiacea) is a monophyletic assemblage and if so, which taxon demarcates its lower limit; (2) whether raninids are part of a monophyletic Oxystomata; and (3) whether the substitution rate for brachyuran 18S rRNA and rDNA is sufficient to resolve relationships among crabs that have recently diverged". These three questions deserve three answers in the light of the present state of knowledge of brachyuran crabs. The first question is:

1. Is the Brachyura a monophyletic group?

The first question contains several sub-questions. The first is: Could the Dromiacea be classified either into the Anomura or into the Eubrachyura (=

Table 1. Differences between the Anomura, the Dromiacea and the Eubrachyura.
Таблица 1. Различия между Anomura, Dromiacea и Eubrachyura.

Character	Anomura	Dromiacea	Eubrachyura
Carapace and epistome	fusion hidden	fusion exposed	fusion exposed
Orbits	absent	absent to present	present
Antennular fossae	absent	absent to present	present
First antennal segment	movable	movable	fixed
Antennal segments 2 + 3	free articulated	fused	fused
Scaphocerite	often present	often present	absent
Third maxilliped (Mxp3)	pediform	operculiform	operculiform
Pereiopods chelate	first or second	first only	first only
Pereiopods 4 and 5	mostly subdorsal	mostly subdorsal	mostly "normal"
Epipods on pereiopods	present	mostly present	absent
Number of gills	numerous (23)	numerous (21 to 7)	reduces (9 or less)
Type of gills	tricho- and phyllobranchs	mostly phyllobranchs	phyllobranchs
Thoracic sternite 8	not fused	fused	fused
Sella turcica	absent	present	present
Spermatheca	absent	present	present
Oviduct and spermatheca	–	separated	connected
Sternal furrows	–	mostly present	absent
Penis	absent	present	present
Female sexual opening	coxal	coxal	sternal
First female pleopod	present	mostly present	absent
Male pleopods 3-5	present	mostly vestigial	absent
Abdominal flexion	incomplete	complete	complete
Uropods	present	vestigial to absent	absent
Abdominal locking mechanism	absent	absent to present	present
Sterno-abdominal cavity	absent	absent	present

Brachyura genuina, = Heterotremata + Thoracotremata)? In order to answer this question, it is necessary to compare the Dromiacea with the Anomura and the Eubrachyura in all the characters used by previous authors [Bouvier, 1940; Balss, 1957; Guinot, 1978; de Saint Laurent, 1979; Burkenroad, 1981] to describe these taxa. The main characters are presented in Table 1.

Because of the marked congruence in the organization between the Dromiacea and the Eubrachyura (in particular, the fusion of the carapace and epistome; the fusion of all thoracic sternites into a sternal plastron; the presence of a *sella turcica*), the Dromiacea should not be included into the Anomura. Nevertheless, it must be mentioned that the larval stages, in particular in the more primitive

Dromiacea, share many anomuran features, as pointed out by some authors [Williamson, 1965; Rice, 1980]. It is worth noting that the Anomura has been differently understood by various authors [McLaughlin & Holthuis, 1985]. For some authors, the Anomura is only the Anomala [Bouvier, 1940; Burkenroad, 1981; de Saint Laurent, 1979], but for other authors the Anomura includes both Thalassinidea and Anomala [Balss, 1957]. Accordingly, it should be noted here that the Anomala has a hidden attachment of the carapace to the epistome under a produced frontal margin, whereas some thalassinids have an exposed fusion of the carapace to the epistome [Burkenroad, 1981]. Thalassinids also have a subcylindrical cephalothorax, a long-extended abdomen with well-developed uropods (forming a tailfan together with the telson), a true rostrum is often present, podobranchs are found on anterior pereiopods (1-3), a scaphocerite is present in some families, well-developed pleopods occur in both sexes, an *appendix interna* is found on the pleopods (2-5), and some have chelae on the second pereiopod, antennulae that are long, cylindrical, straight (not folded), with long flagella, and the palpus of third maxilliped is short. Hence, there is a very distinct gap between the thalassinids and the dromiaceans.

Could the Dromiacea be classified into the Eubrachyura or, as Spears et al.[1992: 448] stated, "the so called "higher" (or "true") crabs", or, as Jamieson [1991: 128] wrote, "the Oxystomata — Oxyrhyncha — Cancridea — Brachygnatha (O-C-B) assemblage or raninoid — heterotreme — thoracotreme assemblage"? As can be seen from Table 1, there is indeed a very distinct gap between the Dromiacea and Eubrachyura. However, it is evident that the gap between the Dromiacea and Anomura is more distinct than that between the Dromiacea and Eubrachyura. Consequently, the systematic position of the Dromiacea remains very isolated in the system of decapod Crustacea. Accordingly, their systematic position remains somewhat problematic because the dromiaceans possess not only many primitive but also very aberrant characters. Namely, all the Dromiacea has, due to an acute dorsal flexion of the posterior sternites, thoracic sternite 8 in a dorsal position, and sternite 7 usually in a vertical or oblique position. Their thoracic sternum is rounded in the sagittal plane and projecting posteriorly behind the posterior margin of the carapace. Furthermore, nearly all their members have the fifth and frequently also the fourth pair of ambulatory legs reduced in size, subdorsal in position and often subchelate or even chelate. Exceptions are the fossil Prosopidae which had a "normal" leg [Beurlen, 1930] and the recently described Poupiniidae [Guinot, 1991] which have the last pair of "normal" structure, i.e. neither subchelate nor conspicuously diminished in length, but only subdorsal in position [Williams & Moffitt, 1991]. Finally, some dromiaceans have very distinct dorsal grooves, particularly the cervical, and often branchiocardiac ones. Only the Homolidae has a pair of longitudinal furrows (*linea homolica*) on the dorsal surface of the carapace. The larvae exhibit a great number of anomuran characters [Williamson, 1965; Rice, 1980], and only the most advanced dromiaceans have a reduced number of anomuran features. Consequently, the Dromiacea is considered as representing aberrant brachyurans.

According to Dollo's law of irreversibility of evolution, structures once lost are not regained. If this concept is applied to the lost "normal" position of the posterior part of the thoracic sternum as well as the size and position of the last two pairs of ambulatory legs, then the higher crabs (Eubrachyura) could have evolved only from crabs with a more or less straight posterior part of the thoracic sternum and a "normal" posterior leg position. This indicates that the Dromiacea is a "cul-de-sac" of evolution [Guinot, 1979] and as such is incapable of being the ancestors to the more derived Eubrachyura. Therefore the question remains: which group was the ancestor of the Eubrachyura? At present no certain answer can be given. However, the data from Table 1 indicate that the Dromiacea and the Eubrachyura split after the basic brachyuran organization had been reached or, in other words, that the Dromiacea diverged early from the main brachyuran lineage.

Which taxon demarcates the lowest limit of the Brachyura, is the next sub-question of Spears et al. [1992]. In order to answer this question, it is necessary to establish, what is an ancestral (original, primitive, plesiomorphic) and what is an advanced (derived, apomorphic) feature in the Dromiacea. The crucial question is, how do we know what is a primitive character state? Crisci & Stuessi [1980] mention the following criteria to be used in ascertaining a primitive character state in the transformation series of a homologous organ: fossil evidence (oldest = primitive), commonness (common = primitive), co-occurrence of primitive states, earliest ontogenetic state, minor abnormalities of organogenesis, vestigial organs, association, correlation and group trends; and here can be added with caution: simple is primitive and complex is advanced (derived) (but not in sedentary or parasitic forms). It should be pointed out that some primitive character states can be reached secondarily by reverse evolutionary pathways. The polarity of the main dromiacean character states (most primitive and most derived) is presented in Table 2.

This approach allows us to propose a natural system for the Dromiacea in which the families with a greater number of primitive character states of various organs are placed at the beginning of the system, and the families with predominantly derived characters at the end. The families with predominantly ancestral characters are the Homolodromiidae and the Prosopidae (fossil), which demarcate the lowest limit of the Dromiacea (the brachyuran

Table 2. Character state polarity within the Dromiacea.
Таблица 2. Поляризация состояний признаков у Dromiacea.

Character	Primitive	Advanced
Cephalothorax form	cylindrical	xanthid-like
Lateral margin	absent	present
Orbits	absent	present
Antennular fossae	absent	present
Scaphocerite	present	absent
Eyes	not protected	protected
Gill number	high (21)	reduced (7)
Type of gills	trichobranchs	phyllobranchs
Third maxilliped	pediform	operculiform
Epipods on pereiopods	1–4	absent
Podobranchs	present	absent
Sternal grooves	present	absent
Posterior pereiopod	"normal"	reduced in size
Endopod of Go1	basally wide	tubular
Second gonopod (Go2)	long	short
Exopod on basis of Go2	present	absent
First pleopod in female	present	absent
Vestigial gonopods 3–5	present	absent
Vestigial uropods	present	absent
Abdominal lock mechanism	absent	present

nature of the Eocarcinidae remains questionable), whereas the most derived dromiacean families are the Cyclodorippidae (=Tymolidae) and the Raninidae. It is noteworthy that there exist no families with all characters at a primitive or only at a derived state. There are always a perplexing mixture of ancestral and derived character states, or the so-called "mosaic evolution", and consequently any higher taxon (at the suprageneric level) is characterized by a specific combination of various character states making an interpretation of their classification difficult.

2. Is the Dromiacea a monophyletic group?

Concerning dromiacean classification, there are still some unresolved questions. One of the conclusions of Spears et al. [1991: 457] is particularly surprising: "The family Dromiidae is not monophyletic". In brachyuran systematics, such artificial groups as Oxystomata, Brachyrhyncha or Brachygnatha have long been known, but they have almost been dismembered by Guinot [1978], while the above statement for the Dromiidae is unexpected. Is the Dromiidae indeed polyphyletic? After a general revision of the family [McLay, 1993], it appears easier to give an answer. According to the present state of knowledge, there is no evidence to suggest dromiid heterogeneity and, therefore, it is likely, we face a monophyletic group, i.e. taxon. The Dromiidae exhibits a considerable diversity in their forms, but concerning their subtaxa, no competent carcinologist has attempted to classify the dromiid genera into tribes and subfamilies. Establishing the character polarity (Table 3) is prerequisite to dromiid classification. Since the character states in the

Table 3. Character state polarity within the Dromiidae.
Таблица 3. Поляризация состояний признаков у Dromiidae.

Character	Primitive	Advanced
Cephalothorax outline	subcircular	subpentagonal
Cephalothorax depth	subglobose	flattened
Dorsal integument	hard	soft
Carapace surface	tomentose	smooth/areolate
Carapace dorsal grooves	distinct	indistinct
Frontal margin	dentate/lobate	rounded/cave-like
Median pseudorostral spine	present	absent
Scaphocerite	long	moderate to absent
Epipods on pereiopods	present	absent
Podobranchs on pereiopods	present	absent
Ambulatory legs	smooth	ridged/nodular
Chelate mechanism on p4 + p5	present	absent
No of propodal spines on p4 + p5	many	few/none
Uropod plates	present	absent
Abdominal segments	non-fused	some fused (6+7)
Vestigial gonopods 3-5	present	absent
Exopod on basis of Go2	present	absent
Telson	rounded	pointed/bifurcate

dromiid genera appear in various combinations ("mosaic evolution"), at present it is very hard to delimit well-defined groups at a subfamily or tribe level with a consistent combination of characters, with the exception of only two aberrant genera, *Hypoconcha* and *Conchoecetes*, which markedly differ from others. Commenting about their position, McLay [1993: 230-231] states: "The main features of the shape of the carapace of *Conchoecetes* are more like those found in other dromiids than in the case with *Hypoconcha*". Namely, *Conchoecetes* differs from other dromiids in having a flattened carapace subpentagonal in outline, the dactyls of the fourth pair of legs large and talon-shaped. Therefore, it might be separated only as a tribe. The genus *Hypoconcha* is characterized by a dorsally depressed and flattened cephalothorax, a membranous dorsal integument, the frontal and lateral margins expanded, concealing the eyes, and the posterior two pairs of legs short, stout, with lunate dactyls. Because of these considerable differences, this genus might be classified as a separate subfamily. In spite of all differences, its organization is dromiid. It is noteworthy that Spears et al. [1992: 457] found that "Bootstrapped parsimony analysis shows such strong support (100%) for a clade consisting of the dromiid crab *H.* (i.e. *Hypoconcha*, rem. Z.S.) *arcuata* and the hermit crab *Clibanarius vitatus* and excluding the other dromiid, *D.* (i.e. *Dromidia*) *antillensis*, that a polyphyletic view of the Dromiidae in particular, and the Dromiacea in general, must be seriously reconsidered". There exists no other evidence confirming such a conclusion. The gap between the Dromiidae and hermit crabs in their overall shape and structure is so deep that their close relation is impossible. Furthermore, Spears et al. stated that a dromiid genus (*Hypoconcha*) is more closely related to a hermit crab (*Clibanarius*) than to another dromiid genus, *Cryptodromiopsis* (reported as *Dromidia*), this deeply contradicting our entire knowledge of brachyuran systematics. The next major problem is the raninids.

3. The problem of the Raninidae

The frog crabs (Raninidae) have long received considerable attention by carcinologists, in particular during the last few decades. The problem of their enigmatic systematic status and position was addressed first by Bourne [1922] and, more recently, by Gordon [1963], and the discussion was continued by Williamson [1965, 1966, 1976]; Hartnoll [1968, 1979]; Stevčić [1973]; Guinot [1978]; de Saint Laurent [1980a, 1980b]; Rice [1980, 1981a, 1981b]; Williams [1984] and, indirectly, in the monographs or reviews of brachyuran systematics by Sakai [1976]; Manning & Holthuis [1981]; Bowman & Abele [1982]; Schram [1986]; Dai & Yang [1991]. During the last three decades, knowledge of the systematics of raninids has augmented considerably due to the investigations of Tyndale-Biscoe & George [1962]; Serène & Umali [1972]; Goeke [1981, 1985]; Davie [1989]; Davie & Short [1989], and Werding & Müller [1990]. Recently, Jamieson [1989, 1991, 1993], Jamieson & Tudge [1990] and Spears et al. [1992] also considered broadly the problem of the systematic position of the raninids.

Now, let me turn to one of the principal topics of the present paper: the systematic position of the family Raninidae. Are the raninids "the most advanced of the primitive Brachyura" [Hartnoll, 1979: 75] or "a member of the Brachyura (sensu stricto) that diverged early from the main brachyuran lineage" [Spears et al. 1992: 456]? Why are there so many discussions concerning the systematic status and position of the Raninidae? First of all, the raninids are extremely aberrant crabs. The frog crabs have the posterior thoracic epimera largely exposed in lateral view (therefore they were named Gymnopleura by Bourne [1922]). They exhibit many atypical characters, predominantly due to their peculiar life-style. The Raninidae is a group of highly modified burying crabs and, like all back-burrowers (and swimmers), they are substantially altered in morphology, with an elongate cephalothorax, an oxystomatous complex: elongate buccal cavern and maxillipeds, respiratory water streams (inhalant aperture between tergum of the first abdominal segment and the coxae of the last pair of pereiopods, exhalant aperture closed by enlarged exopodite and endopodite of the first maxilliped) and a peculiar pereiopod. The Raninidae (with the exception of *Symethis* and *Cyrtorhina*) has flattened chelipeds with fingers of the chela nearly at a right angle to the longitudinal axis of the hand (palm). All ambulatory legs are distally enlarged and flattened, with only the last pair sometimes more or less reduced in size and slightly elevated, but neither typically subdorsal in position (i.e. folded over the back) nor subchelate in a manner like in other Dromiacea carrying a camouflage [Wicksten, 1986], being posed parallel to the posterolateral margin of the carapace. Moreover, the raninids exhibit some characters very atypical for the Dromiacea: their sternum is broadened anteriorly in a highly peculiar shape, and the posterior part is very strongly narrowed and keeled. Paired spermathecal openings, which are situated ventrally in other dromiaceans, due to a narrowing curve of the last two thoracic sternites, are located on the posterior part of the cephalothorax and situated on sternite 7. In the raninids, like in all dromiaceans, the thoracic sternum bends rather abruptly upwards at sternite 6 (bearing the second ambulatory legs or the third pereiopods, respectively). Sternite 7 is nearly vertical, whereas sternite 8 is positioned nearly horizontally. Consequently, the thoracic sternum protrudes posteriorly behind the carapace margin. The consequence of this transformation is that the last pair of legs (P5) is somewhat anterior to P4. The coxae of the last two pairs of legs are visible from above; the abdomen which covers the posterior part of the cephalothorax is largely exposed in dorsal view, being often incompletely or not at all folded under the cephalothorax, a feature unknown in other crabs. Some raninids, e.g. *Lyreidus*, have a flexed abdomen and also a retaining mechanism [Hartnoll, 1975]. Their eyestalks, antennulae, antennae, absent flagellum of the exognath of the third maxilliped and spermathecal openings on sternite 7 are also atypical features for the Dromiacea. Among the Dromiacea, only the raninids have an elongate thoracic ganglionic mass. Their spermathecal openings have attracted special attention [Gordon, 1963, 1966; Hartnoll, 1979; Goeke, 1981] because, at the first glance, they appear to be singular. However, Hartnoll [1979] and Goeke [1981] have established that there are in fact two spermathecal openings which are located at the bottom of a common pit-like depression. Only the genus *Symethis* has two distinctly separated spermathecal openings [Goeke, 1981]. At the same time, the well-formed orbits, the absence of uropods, the sternal furrows, the first ♀ pleopod and the third ♂ pleopod coupled with a reduced number of gills (to 8) confirm the hypothesis that the raninids are highly derived, non-primitive, crabs [Stevčić, 1973]. Finally, the larvae are also peculiar [Williamson, 1976; Rice, 1980, 1981a, 1981b], exhibiting many eubrachyuran characters. Their atypical organization in which they differ from all other crabs is the reason for misunderstandings among carcinologists concerning their systematic status and position. However, the ♀ opening in the coxae of the third pereiopods, the spermathecal opening on the sternum, the structure and size of the first and second gonopods confirm a dromiacean nature of the raninids. It should be added that the elongated cephalothorax, narrow sternum, narrow and elongate buccal cavern and mouthparts are not truly primitive features but only pseudoprimitive ones (i.e. reversals), features gained secondarily as a consequence of their specialized life-style.

Table 4. Character state polarity within the Raninidae.
Таблица 4. Поляризация состояний признаков у Raninidae.

Character	Primitive	Advanced
Frontal border	narrow	wide
Front	triangular	incised
Eyestalk folding	forward	backward
Antennal flagellum	long	short
Merus of Mxp3	not carinate	carinate
Palm of cheliped	swollen	flattened
Spermathecal openings	separated	together
Tubulation of Go1	incomplete	complete
Go2 in relation to Go1	longer	shorter
Extremity of Go2	not ornamented	ornamented
Abdominal locking mechanism	present	absent
Abdominal folding	complete	incomplete

The frog crabs exhibit a considerable diversity [Serène & Umali, 1972; Goeke, 1985] based on a distinct character polarity (Table 4). These data applied to raninid classification permit the conclusion that the genus *Symethis* is the most primitive (the narrow, triangularly projecting front, the nearly "normal" brachyuran chelipeds, two separated spermathecal pits), while *Ranina* and *Cosmonotus* are characterized by advanced characters and therefore should be placed at the opposite end of the raninid hierarchical scheme. How can we consider the unflexed abdomen of the genus *Ranina*? Is it an ancestral (as pointed out by Guinot [1978]) or a secondary attained character [Stevčić, 1973]? There are two pertinent arguments: (1) All the Dromiacea has a flexed abdomen under the cephalothorax, and this means that already at the origin of their evolution the abdomen must have been shortened and flexed under the cephalothorax. (2) The relatives of *Ranina* not only have a more flexed abdomen but some of them, like *Lyreidus*, have developed a retaining mechanism of the abdomen [Hartnoll, 1975]. This indicates that the retaining mechanism has evolved in the raninids and that the genus *Ranina* lost the ability of abdominal flexion during its own evolution. The raninids are isolated from all other dromiacean families, but they remain a dromiacean taxon as the most advanced group. Namely, many raninid organs underwent considerable transformations during their evolutionary history (frontal region, mouthparts, pereiopods, reproductive organs, respiratory system), indicating a longer evolutionary pathway than in other dromiaceans; therefore they must be placed at the end of the dromiacean hierarchical system. The recent findings of Hartnoll [1979], Jamieson [1989, 1991] and Spears et al. [1992] confirm a higher organization level of the raninids. Summing up, the raninids are "the most advanced of the primitive Brachyura" [Hartnoll, 1979: 75] (i.e. Dromiacea) and are not "a member of the Brachyura (sensu stricto) that diverged from the main brachyuran lineage" [Spears et a. 1992: 456] (i.e. Eubrachyura).

4. The problem of Eubrachyura

The Eubrachyura — the largest group of the decapod Crustacea — exhibits an extreme diversity; therefore the question arises, which subtaxa are more primitive and which are more advanced? Table 5 shows the main eubrachyuran character polarities which help to elucidate this problem. Since primitive character states of many homologous organs predominate in the families Atelecyclidae, Cancridae, Thiidae and Corystidae, their position should be at the beginning of the brachyuran hierarchical system, while the families with a maximal number of derived (advanced) character states of many organs are in the families Hymenosomatidae, Cryptochiridae, Ocypodidae and Mictyridae, so these families should be placed at the end. It is worth noting that the most primitive families are often classified together into the superfamily Cancroidea

Table 5. Character state polarity within the Eubrachyura.
Таблица 5. Поляризация состояний признаков у Eubrachyura.

Character	Primitive	Advanced
Cephalothorax form	subhexagonal	subquadrangular
Regions of carapace	distinct	indistinct
Front	narrow	wide
Posterior carapace margin	narrow	wide
Antennular folding	longitudinally	transversely
Orbital hiatus	open	closed
Buccal cavity	quadrangular	triangular
Insertion of Mxp3 palpus	antero-internal	antero-external
Posterior pair of legs	"normal"	modified
Male sexual opening	coxal	sternal
Sternal sutures 4/5 — 7/8	continuous	interrupted
Abdominal segments	unfused	fused
Thoracic sternum	narrow	wide
Sterno-abdominal cavity	absent	present
Second gonopod (Go2)	longer than Go1	shorter than Go1

(= Corystoidea). However, it is known that: "The possession of plesiomorphous characters (symplesiomorphy) does not justify the conclusion that the bearers of these characters form a monophyletic group" (Hennig, 1966: 90). The co-occurrence of primitive characters in the above-mentioned families does not justify the statement that the Cancroidea is a natural group. Indeed, Miers [1886: iv] considered the Corystoidea as a "somewhat heterogeneous group".

Another subquestion refers to the Oxystomata. Miers [1886: ix] likewise expressed his doubts that the Oxystomata is a natural group ("a somewhat heterogeneous group, which it will perhaps be found hereafter impossible to sustain its entirety"), but despite all doubts, carcinologists have continued to use the group. In contrast, Guinot [1978] dismembered it. However, although she rejected the old classification, her classification of the higher crabs commenced with the Dorippidae. Unfortunately, her evidence for a reclassification of the Oxystomata was not sufficiently convincing to the scientific community of carcinologists, so we can still find this group name in use in recent monographs dealing with crabs. The same could be said about the Oxyrhyncha [Guinot, 1978; Stevčić & Gore, 1981; Rice, 1980, 1981a] which is also a polyphyletic group but not abandoned by the majority of carcinologists. Jamieson [1991] and Spears et al. [1992] have also confirmed their heterogeneity. The third question of the latter authors is:

5. Molecular biology and brachyuran systematics

Is the substitution rate for brachyuran 18S rRNA and rDNA sufficient to resolve phylogenetic relations among the crabs? Similar to all other pieces of evidence of relationships, single characters are insufficient to solve complex phylogenetic problems. The greater the evidence, the greater the justification for inferences. In systematics, there is neither philosophers stone, i.e. an absolute criterion for all systematic questions, nor such a criterion which would not lead to an artificial system. Consequently, new evidence for a classification, including ultrastructural and molecular, is as welcome as all other morphological, physiological and ecological evidence. Accordingly, it will be useful to analyze the spermatozoan ultrastructure and 18S rRNA and DNA of a greater number of representatives of all brachyuran families, subfamilies and enigmatic genera and thus promote a solution of some systematic problems. However, an analysis of 18S rRNA sequence data is insufficient for taxonomic research but, in combination with other methods, it could perhaps yield a useful evidence for systematic inferences. Unfortunately, no conclusion obtained by Spears at al. [1992] is in accordance with the classical hierarchical system of the crabs. Phyletic evolution, which results in the brachyuran hierarchical system, is very complex, including structural, functional and adaptive aspects, and the use of only one character or group of characters aspect can easily lead to an artificial system.

The final conclusion of Spears et al. [1992: 458] is the following: "The results of molecular, spermatozoan and larval studies are consistent with one another". However, as shown above, there are no discordances in the results of the contemporary brachyuran systematics based on the homologies of adult crabs. At present I am able to find no agreement between the results obtained by an analysis 18S rRNA sequences and the brachyuran system obtained by classical methods. How can this disagreement be explained? According to the present state of knowledge of brachyuran systematics, we are unable to answer questions such as, for example, the relationships between ontogenetic (larval), cellular, molecular, and phyletic evolution. We know very little about the evolution of higher taxa. Recently, carcinologists have focused their primary attention to alpha taxonomy, while the higher taxa have been almost neglected. The majority of systematists still use the "pre-diluvial" classification which includes groups such as Oxystomata, Brachygnatha, Oxyrhyncha and Brachyrhyncha which are not true taxa but only artificial assemblages based on some superficial similarities (convergences and parallelisms). The first task of brachyuran systematics should be a revision of the extinct and extant taxa, their complete redescription and reclassification [Stevcic, in preparation]. This is a prerequisite for all further investigations in brachyuran systematics and evolution.

Jamieson [1991] made a step forward by applying ultrastructural morphology to brachyuran systematics and phylogenetics. Jamieson's findings (summarized in his fig. 5) agree in *grosso modo* with the system proposed by Guinot [1978], and the differences with the classical system based on the homology of organs are only minor. For example, the Dromiidae (as more primitive) and the Raninidae (as more derived) are classified into the Podotremata (= Dromiacea), while the Majidae, Calappidae, Portunidae, Dorippidae and Xanthidae are classified into the Heterotremata. According to our knowledge of brachyuran systematics, the Xanthidae is more primitive than the other above families, but no close relationships between Majidae and Calappidae, and between Portunidae and Dorippidae, could be confirmed. Furthermore, he correctly classified Ocypodidae, Mictyridae and Grapsidae into the Thoracotremata but isolated the Macrophthalminae from the Ocypodidae as the most primitive thoracotremate group. According to the present knowledge, among the studied taxa, the Grapsidae is the most primitive, and the Mictyridae the most advanced, Thoracotremata. In his last attempt, Jamieson [1993] has substantially approached the classical view of brachyuran classification. His most important conclusions are the following: " (1) "The Brachyura is a monophyletic taxon", and (2) "The Podotremata is a monophyletic taxon and the sister group of the heterotreme-thoracotreme assemblage" (p. 34). Or, in other words: The Dromiacea is the sister group for the Eubrachyura. This is consistent with the views presented here.

Conclusions

In the present contribution, some outstanding problems concerning the fundamental classification of brachyuran higher taxa have been treated. Despite the fact that we are not able to answer all the questions raised, and in spite of many uncertainties and controversies, it is clear that: It would not be justified to exclude the Dromiacea from the Brachyura; the Raninidae is a part of the Dromiacea, with currently no certain indication that the Dromiidae represents a polyphyletic group. And what is the final result of this discussion? In fact: *status quo ante bellum*. Nevertheless, if nothing more, a temporary re-examination of the outstanding problems with a new argumentation useful for an elucidation of some misunderstandings among the carcinologists. At the same time, this discussion of unresolved problems indicates that we have to pay more attention to the problems of higher taxa and, step by step, find proper solutions.

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