

The spider chelicerae: some problems of origin and evolution

Хелицеры пауков: проблемы происхождения и эволюции

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ABSTRACT. Some problems of the origin and evolution of the chelicerae in spiders are discussed. The enlargement and bending of the basal cheliceral segments combined with the displacement of the fang insertion point ventrad is recognized as the principal cheliceral modification observed in the Araneae. The chelicerae of the Liphistiidae and the Mygalomorphae are regarded as plesiomorphic in their position and axial orientation, but as apomorphic by their configuration; the latter seems to be an evolutionary compromise caused by burrowing activity. The possibility of an origin of the labidognathous cheliceral construction from the specialized orthognathous chelicerae of liphistiids and mygalomorphs is regarded as improbable.

РЕЗЮМЕ. В статье обсуждаются вопросы происхождения и эволюции хелицер у пауков. Основными модификациями хелицер, наблюдаемыми у ортогнатных пауков, признаются укрупнение и выгибание основных члеников хелицер и смещение точки прикрепления коготка на их вентральную сторону. Хелицеры Liphistiidae и Mygalomorphae принимаются плезиоморфными по занимаемому положению и осевой ориентации, но апоморфными по своей конфигурации; последняя представляется результатом эволюционного компромисса, вызванного переходом к норному образу жизни. Возможность происхождения хелицер лабидогнатного типа из специализированных ортогнатных хелицер лифистиид и мигаломорфов признается маловероятной.

KEY WORDS: Araneae, spiders, chelicerae, evolution.

КЛЮЧЕВЫЕ СЛОВА: Araneae, пауки, хелицеры, эволюция.

Introduction

Until recently the traditional standpoint treating the cheliceral construction in the orthognathous spiders as an initial state of the labidognathous chelicerae was dominant and used in a great number of arachnological publications [see Platnick & Gertsch, 1976]. All those works

considered (explicitly or by implication) the orthognathous chelicerae in spiders as precursors of the labidognathous type. Starobogatov [1985] also used a third category, plagi axiality, a somewhat intermediate cheliceral orientation occurring in the Hypochiloidea. Otherwise, his reconstruction was given in the traditional style: orthognathy–plagi axial state–labidognathy.

Kraus & Kraus [1993] first arrived at the conclusion that not only labidognathous chelicerae, but also the orthognathous cheliceral construction represented the apomorphic modifications of a primary type defined as the plagi axial variant. In their opinion, this model can be represented in all main lineages of the order Araneae. The cheliceral configurations known for the Liphistiidae, for a number of mygalomorph taxa possessing shorter chelicerae, and for the representatives of the family Hypochilidae, were considered as the most similar to the mentioned type.

Dunlop [1997] supported this hypothesis and added a new state, palaeognathy, found in members of the fossil Paleozoic order Trigonotarbida. He suggested that both orthognathy and labidognathy can be derived from palaeognathy through the plagi axial type by simple torsions of basal cheliceral segments, and some particular states can be explained by reversals.

However, the palaeognath–plagi axial version appears to be only one of a few possible ways of explaining the situation observed. A new attempt to restore the idea to separate the orthognaths and labidognaths from each other was made by Eskov & Zonstein [1990a]. A little later, I demonstrated another scheme showing the independent origin of orthognathous and labidognathous chelicerae in spiders at the Third Eurasian Arachnological Conference. This report was briefly reviewed by Mikhailov [1992], but it has never been published. Despite the general formal resemblance of both hypotheses, they were based on quite different assumptions and a number of the significant differences between them could be listed. The expanded and reworked variant of the 1992 version is given here.

Material and methods

A noticeable part of the material used for this study was lent from the spider collection of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, in the early 1990s. It included numerous mygalomorph taxa belonging to the families Atypidae, Idiopidae, Actinopodidae, Ctenizidae, Cyrtachenidae, Hexathelidae, Dipluridae, Nemesiidae, Barychelidae and Theraphosidae. In addition, material was kindly sent to me by Dr. Kirill Eskov (*Heptathele*) and Dr. Frederick Coyle

(North American mygalomorphs including representatives of the Antrodiaetidae, *Microhexura*, etc.). Also examined were some taxa of the Uropygi and the Araneomorphae. The majority of whip spider specimens used, a few females representing two species of *Liphistius*, and a specimen of *Hypochilus coylei* (all from the collection of the American Museum of Natural History) were kindly lent to me for study through the courtesy of Dr. Norman Platnick.

Most of the figures were prepared specially for this study. Additionally, I had to use some drawings taken from other sources, all these were scanned so that the output was changed minimally from their original form. In a few extraordinary cases some figures were redrawn from the original source. All credits and relevant references are provided.

With minor exceptions, the terminology follows Kaestner [1956], Starobogatov [1985], Shultz [1990], Kraus & Kraus [1993] and Dunlop [1994, 1996c, 1997]. The subbasal cheliceral segment corresponds to the cheliceral coxa of lower arachnids, absent in spiders and their Recent relatives [see Dunlop, 1997].

Some terms as well as the states denoted should be specified. The term *plagi axial* is used only in cases when the cheliceral fangs meet each other at approximately 90°, axial orientation of the basal cheliceral segments occupies an intermediate position between the forward-directed and downward-directed types; these axes are divergent laterally. The terms *palaeognathy*, *plesiognathy* and *neognathy* as well as the derived forms (e.g., *plesiognathous*) are used to designate the orthognathous states found in the Trigonotarbida, in the Pedipalpi (that includes the orders Amblypygi, Uropygi and Schizomida) and in the Araneae, respectively. The first term (palaeognathy) was first used by Dunlop [1997], whereas the latter two are newly applied to the arachnids. The swollen neognathous chelicerae are characterized by the claw insertion point displaced ventrad [Dunlop, 1994: fig. 1]. The least modified plesiognathous construction retains many ancestral characters including a trapezoidal basal cheliceral segment provided with a toothed vestige of the former immovable finger [Dunlop, 1994: figs 2, 3]. Finally, the palaeognathous cheliceral configuration includes both the fangs more or less displaced, and the general cheliceral orientation changed from forward- to downward-directed [Dunlop, 1994: fig. 4].

The term *phrynid type* applies only to the generalized subchelate construction occurring in the Recent taxa represented by the Amblypygi, the Uropygi, the Schizomida, and found to be applicable also for some members of the fossil order Trigonotarbida (for details see the corresponding parts of this study).

This term reflects a certain evolutionary level only; it does not convey any taxonomic context.

Results and discussion

Origin

The allied groups

Most phylogenetic studies agree in placing Araneae into the same group with Amblypygi, Uropygi and Schizomida — other arachnid orders with members also possessing two pairs of book-lungs and the clasp-knife-shaped chelicerae¹. Together they constitute the Tetrapulmonata Shultz, 1990. Some disagreement occurs only in drawing spiders closer to one or another subtaxon within this group.

Until recently Amblypygi were found to be the closest relatives of spiders [see Platnick & Gertsch, 1976]. Most often Uropygi *s.lat.* (Telyphonida + Schizomida) has been considered a sister group of this pair [Grasshoff, 1978; Weygoldt & Paulus, 1979; Wheeler & Hayashi, 1998]. On the other hand, Shultz [1990] followed Pocock's [1893] scheme proposing a closer relationship between Amblypygi and Uropygi *s.lat.*; Araneae was recognized to be an adelphotaxon of this group. Palaeontological studies also supported the latter model [except Selden, 1996a] and included in the Tetrapulmonata the fossil order Trigonotarbida [Shear *et al.*, 1987; Selden *et al.*, 1991; Selden & Dunlop, 1998].

Among recent studies considering or touching upon the problem, some grouped Amblypygi with Uropygi [Giribet *et al.*, 2002], some treat both above hypotheses as equally competitive [see Miller, 2003], whereas others do not clearly prefer either of them [Harvey, 2002, 2003]. In this study the possibility of drawing spiders together with both alternative groups is also taken into consideration, although the position of Shultz [1990, 1999] and subsequent authors is found to be more substantiated.

¹ Within the Arachnida only ricinuleids also possess two-segmented subchelate chelicerae of similar shape [see Dunlop, 1996c: fig. 11].

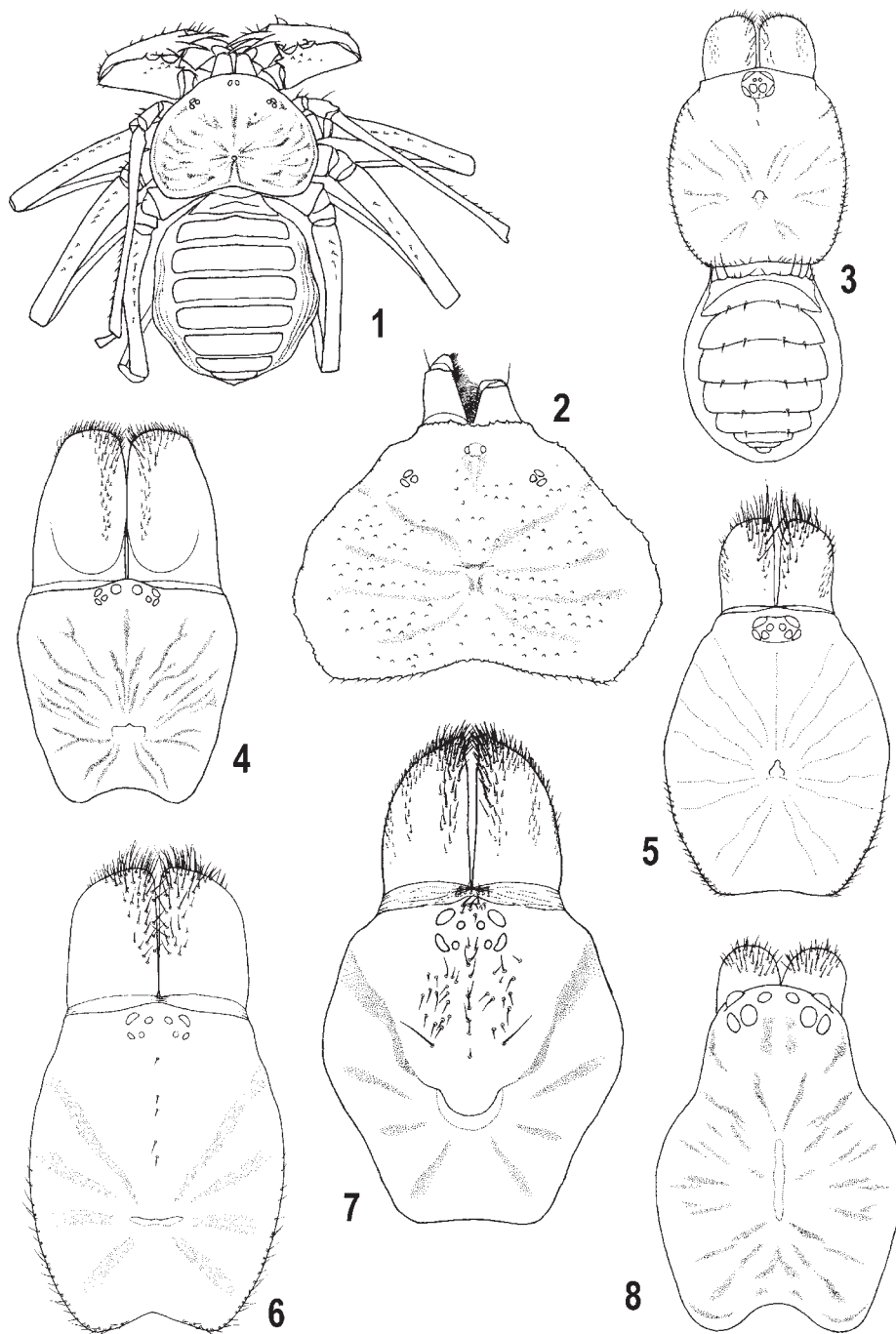
Pedipalpi

Plesiomorphically, ancestors of the Tetrapulmonata presumably possessed three-segmented, chelate chelicerae with the movable finger (the future tetrapulmonate cheliceral fang) located retrolaterally; it is the cheliceral construction that is shared by the less advanced arachnids, including representatives of the order Palpigradi adjacent to the tetrapulmonates [Dunlop, 1997; Selden & Dunlop, 1998].

The orthognathous chelicerae occurring in the representatives of those orders were considered to be the most archaic cheliceral construction occurring within this pair of taxa. The main constructive features of this type are as follows: (1) contrary to spiders, the chelicerae here are relatively small (cf. Figs 1–8); (2) basal cheliceral segments are trapezoidal and flattened; (3) the fang is relatively short and joined to the basal segment close to its foremost dorso-apical vertex; (4) the toothed part of cheliceral furrow representing a vestige of the former immovable cheliceral finger is also rather short, it does not extend to the basal cheliceral margin; (5) unlike other tetrapulmonate orders the fang is more or less toothed — a symplesiomorphy shared with more archaic arachnids.

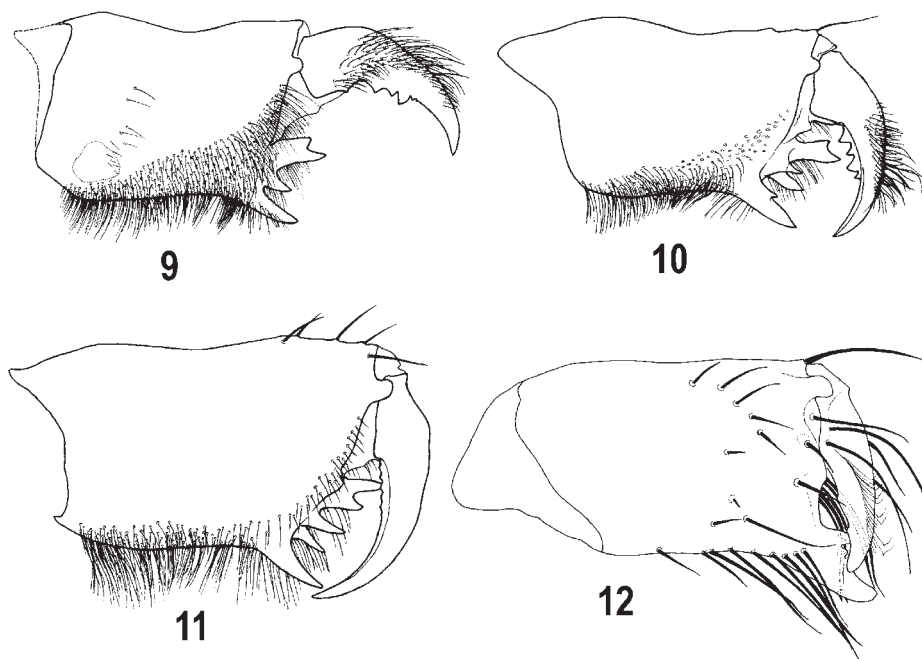
Theoretically, a variant just like this would underlie the construction of the neognathous spider chelicerae because it appears to represent a certain intermediate state between the chelate construction of more archaic arachnids and the piercing spider type. This intergrade can be derived from the archetype by rotation of the basal cheliceral segments around their axes so that the movable cheliceral finger changes its position from anteroretrolateral to anterodorsal. In some advanced arachnid orders other than higher tetrapulmonates a contrary torsion is present; thus, Pseudoscorpiones and Solifugae share the movable finger displaced completely or partially ventrad.

However, according to Kraus & Kraus [1993], some data allow the assumption that orthognathy in the Pedipalpi and the Araneae could have a different origin. They noted that unlike the spiders at least the amblypygids possess a proximal cheliceral apodema arising retrodorsally; correspondingly, there are certain differences in the retracting musculature ar-



Figs 1–8. Chelicerae — dorsal view and comparative dimensions in some whip spider and spider taxa: 1 — *Charinus* sp.; 2 — *Paraphrynus mexicanus* (Bilimek); 3 — *Liphistius panching* Platnick et Sedgwick; 4 — *Atypus* sp.; 5 — *Phyxioschema* sp.; 6 — *Anemesia karatauvi* (Andreeva); 7 — *Cteniza* sp.; 8 — *Hypochilus coylei* Platnick.

Рис. 1–8. Хелицеры — общий вид дорзально и сравнительные размеры в некоторых таксонах фрино и пауков: 1 — *Charinus* sp.; 2 — *Paraphrynus mexicanus* (Bilimek); 3 — *Liphistius panching* Platnick et Sedgwick; 4 — *Atypus* sp.; 5 — *Phyxioschema* sp.; 6 — *Anemesia karatauvi* (Andreeva); 7 — *Cteniza* sp.; 8 — *Hypochilus coylei* Platnick.



Figs 9–12. Chelicerae of whip spiders and schizomids: 9 — *Paraphrynus mexicanus* (Bilimek); 10 — *Phrynus marginemaculatus* C.L. Koch; 11 — *Charinus* sp.; 12 — *Stenochrus portoricensis* Chamberlin [after Tourinho & Kury, 1999: fig. 5]; 9, 12 — retrolateral view; 10, 11 — prolateral view.

Рис. 9–12. Хелицеры фринов и схизомид: 9 — *Paraphrynus mexicanus* (Bilimek); 10 — *Phrynus marginemaculatus* C.L. Koch; 11 — *Charinus* sp.; 12 — *Stenochrus portoricensis* Chamberlin [по Tourinho & Kury, 1999: fig. 5]; 9, 12 — ретролатерально; 10, 11 — пролатерально.

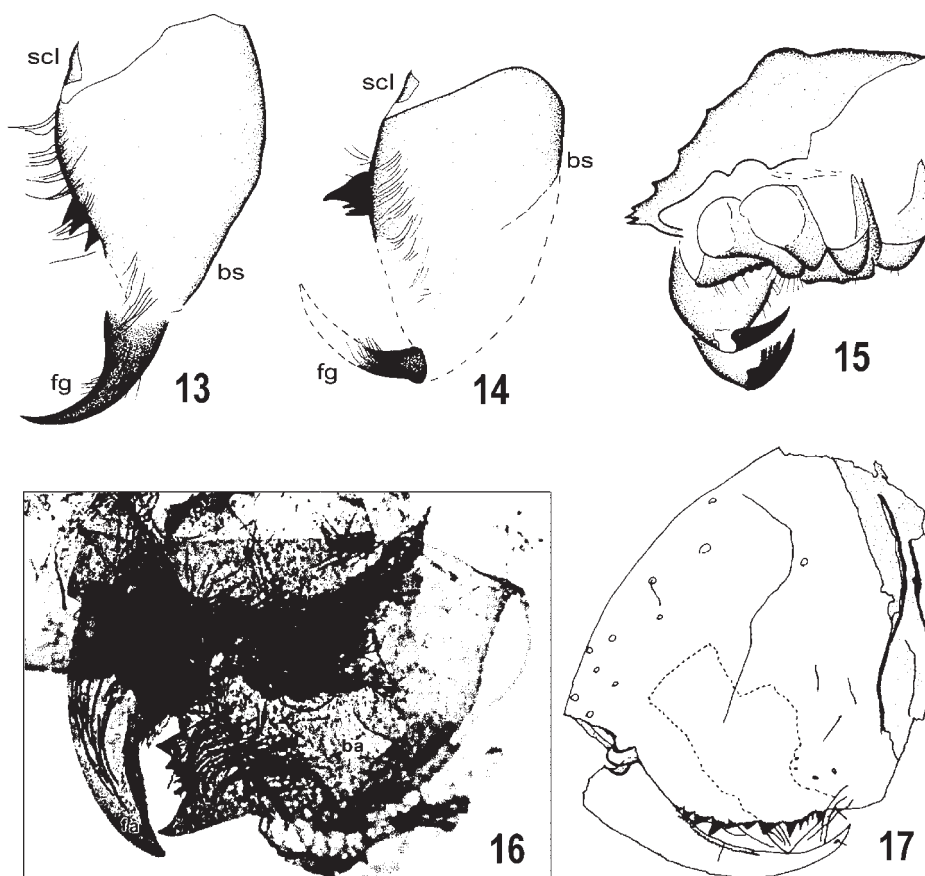
rangement. A similar structure is evident in the schizomid cheliceral construction (Fig. 23). These observations could potentially indicate the noticeable structural differences between two types of orthognathous chelicerae.

On the other hand, it should be noted that the representatives of many spider families possess a similar cuticular cheliceral process, though in the less developed or in the rudimentary form, and located medially or prodorsally. In the spider taxa examined it was absent only from the representatives of higher araneomorphs (Entelegynae). Both its reduction and overgrown development (as in the Filistatidae) appear to be innovative. Therefore, it seems that the presence of a large retrodorsal cheliceral process in the Pedipalpi does not belong to the principal definitive characters; it could be considered an additional cheliceral modification shared by members of this group.

Trigonotarbida

Trigonotarbids, fossil Paleozoic arachnids, constitute one more order known for their clasp-knife-like chelicerae [Shear *et al.*, 1987; Dunlop, 1994]. The order was found to be a sister group of other tetrapulmonates [Dunlop, 1996b; Selden & Dunlop, 1998]; at the same time it shows some relationship to the Ricinulei [Dunlop, 1996c]². But despite the proposed position, the Trigonotarbida has never been re-

² Both Trigonotarbida and Ricinulei share some possible synapomorphies as well as the partially or entirely hidden chelicerae [Dunlop, 1996c]. The problem is that the last order is generally placed into the same branch with the Acari, far away from the Araneae and its relatives [Weygoldt & Paulus, 1979; Shultz, 1990, 1999; etc.]. Moreover, exactly this union is the most concordant clade shared by a number of the otherwise conflicting arachnid cladograms proposed by different authors [see Wheeler & Hayashi, 1998; Harvey, 2002]. Otherwise, Giribet *et al.* [2002] consider the union of Trigonotarbida and Ricinulei to be more substantiated.



Figs 13–17. Chelicerae of trigonotarbids and ancestral pre-mesothele spiders: 13–15 — some modified variants occurring in trigonotarbids [Dunlop, 1997: fig. 4]; 16 — *Gelasinotarbus reticulatus* Shear, Selden et Rolfe, prolateral view [Shear *et al.*, 1987: fig. 68]; 17 — *Attercopus*, the same position [Selden *et al.*, 1991: fig. 4c]. Abbreviations: *bs* = basal cheliceral sclerite; *fg* = cheliceral fang; *scl* = vestigial first (subbasal) cheliceral sclerite.

Рис. 13–17. Хелицеры тригонотарбид и пред-лифистиоморфных пауков: 13–15 — некоторые модификации хелицер у тригонотарбид [Dunlop, 1997: fig. 4]; 16 — *Gelasinotarbus reticulatus* Shear, Selden et Rolfe, хелицера пролатерально [Shear *et al.*, 1987: fig. 68]; 17 — *Attercopus*, то же [Selden *et al.*, 1991: fig. 4c]. Сокращения: *bs* = базальный склерит хелицер; *fg* = коготок хелицеры; *scl* = рудимент первого (суббазального) хелицерального склерита.

ferred to the same lineage as the Araneae [see Selden *et al.*, 1991; Dunlop, 1996c].

Like the representatives of Amblypygi and Uropygi, trigonotarbids possessed rather small orthognathous chelicerae, which were strongly flattened bilaterally [Shear *et al.*, 1987; Dunlop, 1996a]. A few of them also possessed a vestige of the third (subbasal) cheliceral segment that is absent in the extant tetrapulmonate orders [Dunlop, 1997]. In some trigonotarbid taxa the general shape of the chelicerae resembled the configuration of the mygalomorphs, however, the trigonotarbid chelicerae were

paraxial but directed downwards, as in higher araneomorph spiders (cf. Figs 13–15, 22–25). Dunlop [1997] described this as palaeognathy and supposed that it represents a precursor of the plagiaxiality in spiders developed later, according to the O. & M. Kraus' hypothesis, into the orthognathy of most mygalomorphs and the labidognathy of the more advanced araneomorphs, respectively. In this scheme the opposing phrynid type represents a synapomorphy shared by the Amblypygi and the Uropygi *s.lat.* In most respects however, the last construction appears to be less modified than both men-

tioned earlier (see above). Hence, either trigonotarbid and spider chelicerae should be treated as developed independently from each other, or the phrynid type shared by other tetrapulmonate arachnids has to be considered a reversal. The last option seems to be less preferable than the first for the reasons given below.

First, such a reversal should affect not one but several characters at once: the general configuration of the basal cheliceral joint, the shape of the cheliceral furrow, the fang shape and configuration, the locus of the fang insertion point, as well as a general axial orientation of the chelicerae. Second, the mentioned phrynid state corresponds more to the transitional variant joining the palpigrade and spider conditions, as was noted above. The last event could be explained more parsimoniously by assuming this intermediate structure as the most archaic construction, common for tetrapulmonate arachnids.

If the union of the Trigonotarbida and the Ricinulei actually represents a clade, not a grade, one more contradiction is evident. Although the ricinuleids also possess the downwards-hanging chelicerae, their construction seems to be distinctly more archaic than that of the trigonotarbids. Besides the mobile cheliceral finger, it possesses also the immobile one, though in a reduced form. The last detail has been lost in the trigonotarbid chelicerae which calls for one more reversal in the ricinuleids. Therefore, potentially this union can pose some additional obstacles for recognizing palaeognathy as a pre-neognathous condition.

Besides, the trigonotarbid chelicerae with the most pronounced palaeognathy show greater similarity to the mygalomorph variant, rather than to the liphistiid and hypochiloid states (Figs 13–15). They also differ notably from the cheliceral construction known for the most ancestral spiders (see below). Most probably, their narrowed form and the unique axial orientation have been caused by encapsulating (together with bases of other appendages) into a tight testaceous carapace provided with a hypertrophied downward-inclined clypeus — as shown from the trigonotarbid reconstructions figured by Shear *et al.* [1987], Dunlop [1996a], etc. In the orthognath spiders possessing the carapace more open fron-

tally, the analogous cheliceral modifications could not be caused inevitably by the same evolutionary factors as in the trigonotarbids. The presence within the Trigonotarbida of some less specialized forms with chelicerae weakly distinguishable from the phrynid type³ (Fig. 16), provides reliable evidence in favour of this viewpoint.

Pre-mesothele fossil spiders

Almost all Paleozoic ‘orthognath’ and ‘labidognath’ spiders described prior to the end of the 1980s, later were shown to either belong to other arachnid orders or to be outside the chelicerates altogether [Starobogatov, 1985; Eskov & Zonstein, 1990a,b; Selden *et al.*, 1991, 1999]. Unlike those taxa, the Devonian *Attercopus* was described possessing both spinnerets with functional spigots and the cheliceral glands, which confirmed its membership in the Araneae [Selden *et al.*, 1991]. These authors specially noted for *Attercopus* the first appearance of a naked cheliceral fang representing a typical spider feature (in all other tetrapulmonates it is plesiomorphically covered with setae or hairs, cf. Figs 9–16). Its uniqueness in certain characters (the absence of the trichobothria, etc.), makes this taxon distinct from all other spider groups [Selden *et al.*, 1991: fig. 3; Selden, 1996a: fig. 5a].

With the exception that the chelicerae of *Attercopus* were noticeably shorter, they resemble in general those of the liphistiomorphs: the basal segment with an arched upper part and the fang inserted closer to its ventral surface; a toothed part of the cheliceral furrow extends along the full length of this structure; the fang extends backwards horizontally (Fig. 17). In contrast to the plagi axial type, they were distinctly flattened prolaterally; the dorsal part of the basal sclerite was swollen and slightly mound-like [Selden *et al.*, 1991: Pl. 1, fig. 6]. Finally, it should be emphasized that the highly orthognathous construction seems to be equally suitable as a basis for both the modified orthognathous and plagi axial types.

³ Those isolated chelicerae imprints could belong, in principle, to a fossil arachnid taxon outside the Trigonotarbida. However, the authors of that study suggested that they should be attributed to the fragmentary known trigonotarbid *Gelasinotarus reticulatus* “either by association with carapace fragments or by having characteristic sculpture” [Shear *et al.*, 1987: p. 39].

Principal modifications

Mesothelae

The main features of the cheliceral configuration in *Heptathela* and *Liphistioides* are: the modified (swollen) dorsal lobe of the basal segment; displacement of a fang attachment point closer to its ventral surface; lengthening of the cheliceral furrow. Despite the fact that such a construction appears to be very similar to the general shape of the chelicerae in the mygalomorphs, lateral surfaces of the basal segments in liphistiids appear less convex (i.e., more similar to the types observed in the representatives of other tetrapulmonate orders, Figs 1–3). All the available liphistiid specimens as well as photographs of live mesothelid spiders show that they never hold their chelicerae expanded laterally, as was figured by Bristowe [1933: Pl. 5, fig. 9]. Like most mygalomorph spiders, the Recent representatives of the Liphistiidae are burrowers [see Platnick & Sedgwick, 1984; Ono, 1999].

According to Kraus & Kraus [1993], the liphistiid chelicerae lie close to the plagi axial model typical for *Hypochilus*. However, when compared these variants show strong evidence that the mesothelid state resembles the orthognathous pattern occurring in the mygalomorphs, rather than the plagi axial chelicerae of the Hypochiloidea (cf. Figs 17–24 and 32). The same relationship is characteristic for the Upper Carboniferous mesothelid *Paleothele*, whose chelicerae belong to the paraxial type [Selden, 1996a⁴,b].

Judging from the description, the chelicerae of *Paleothele* were rather small, they appear to be smaller than chelicerae in the Recent representatives of the group [see Selden, 1996a: fig. 3b]. Unfortunately, the poor preservation of the cheliceral parts in these fossils does not give an opportunity for their unequivocal reconstruction. Even so, in shape they definitely differ from both the phrynid type and the plagi axial chelicerae of hypochiloids. The fang position in *Paleothele* seems to be modified and translocated clearly closer to the ventral side of the basal cheliceral segment. Besides, the fossil mesothelid spider possessed a long cheliceral

furrow with two tooth rows aligned throughout the whole length of this structure.

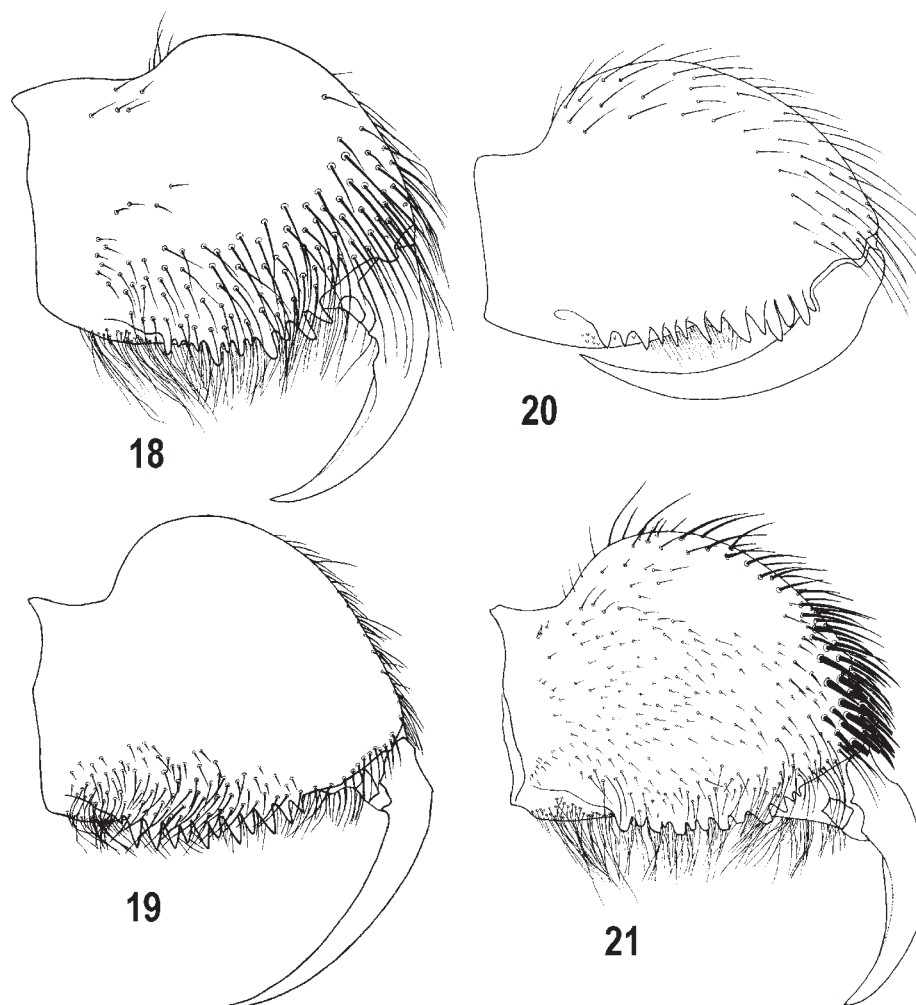
Although those characters do not support a close resemblance between the liphistiid and hypochiloid chelicerae, they give ample basis for further cheliceral modifications in the mygalomorphs.

Mygalomorphae

The generalized shape of the chelicerae in mygalomorphs differs only a little from that occurring in the Mesothelae. The most noticeable detail of this shared construction is a swollen dorsal lobe of the basal segment; as a result the fang attachment point is confined to its ventro-apical vertex vs. a primary dorso-apical position (Figs 18–25). When compared with cheliceral construction in the liphistiids, the mygalomorph chelicerae appear in general to be noticeably more highly modified. Additional modifications which occurred in the Mygalomorphae are: (1) enlarged chelicerae in most members of the Fornicephalae *sensu* Raven, 1985, achieving their maximum size in the representatives of the Atypidae; (2) short chelicerae of Migidae and some Actinopodidae, and (3) somewhat diminished chelicerae in web-building mygalomorphs of the families Dipluridae and, in part, Mecicobothriidae and Hexathelidae. It should be noted that unlike the specialized burrowing mygalomorphs (but close to the Recent liphistiids), the basal cheliceral segments in the representatives of the latter families are mostly geniculate, not convex laterally (as shown in Fig. 5).

In diplurids the chelicerae vary in the related species from rather large to small, even within the same genus [cf. Raven, 1984a: figs 45–51, 124–139; Coyle, 1988: figs 15, 16]. However, genera wholly known to possess small chelicerae with a ‘lesser orthognathy’ (*Microhexura* Crosby et Bishop, *Chilehexops* Coyle) have at the same time some other characters in a clearly derived or reduced form. These include the number of eyes or spines, or the construction of the male mating spur [see Coyle, 1981, 1986]. Within the mecicobothriids the less developed chelicerae somewhat resembling the plagi axial construction are known for the most advanced genus *Hexurella* Platnick et

⁴ First described under *Eothele* Selden; later a new name was proposed in view of the homonymy [Selden, 2000].



Figs 18–21. Chelicerae of liphistiids and primitive mygalomorphs, prolateral view: 18 — *Liphistius malayanus* (Abraham), Liphistiidae; 19 — *Megahexura fulva* (Chamberlin), Mecicobothriidae [from Gertsch & Platnick, 1979: fig. 56; modified]; 20 — *Atypus* sp., Atypidae; 21 — *Antrodiaetus unicolor* (Hentz), Antrodiaetidae.

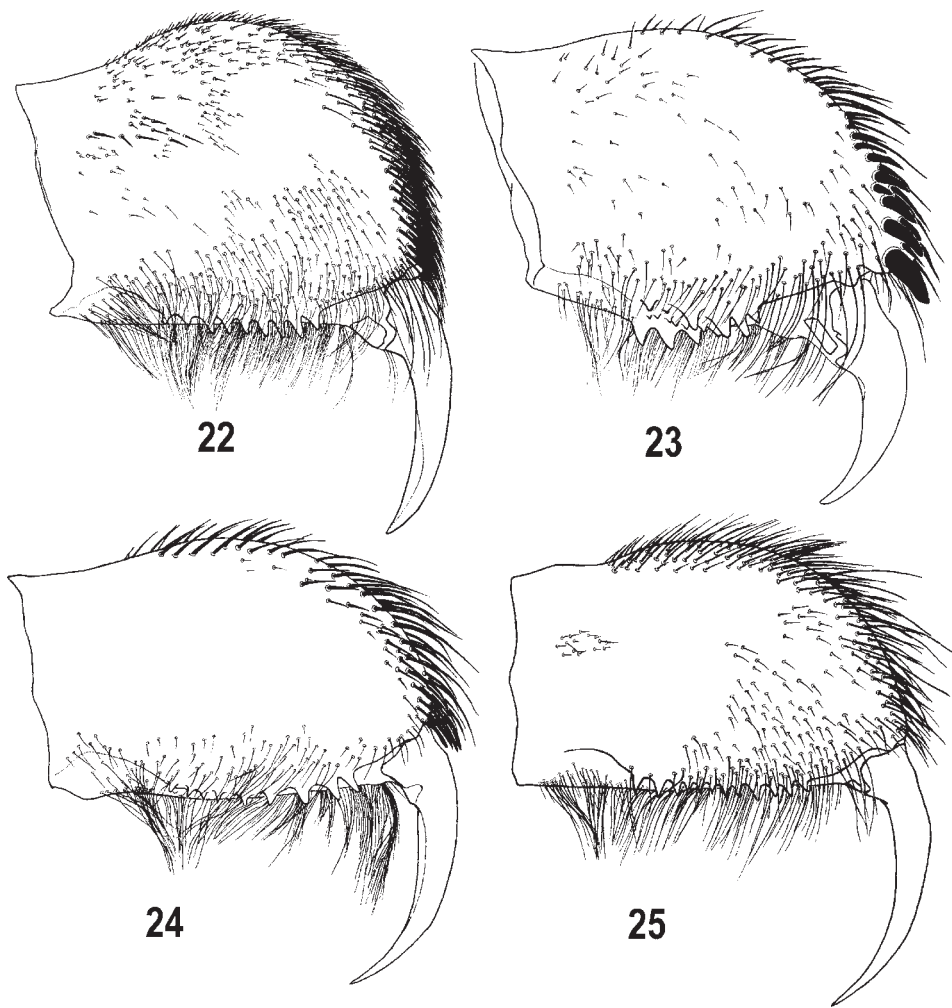
Рис. 18–21. Хелицеры лифистиид и примитивных мигаломорфов, пролатерально: 18 — *Liphistius malayanus* (Abraham), Liphistiidae; 19 — *Megahexura fulva* (Chamberlin), Mecicobothriidae [по Gertsch & Platnick, 1979: fig. 56; изменено]; 20 — *Atypus* sp., Atypidae; 21 — *Antrodiaetus unicolor* (Hentz), Antrodiaetidae.

Gertsch, whereas three, more archaic genera possess the strictly orthognathous large chelicerae [cf. Gertsch & Platnick, 1979: figs 35–37, 51–53, 58–60 vs. figs 70–73]. The more advanced position of the first genus was confirmed by Raven [1985].

The web microstructure in diplurids somewhat differs from that known for the araneomorph spiders [see Palmer, 1985], but at the same time is indistinguishable from the burrow silk lining. Thus, it could be logically assumed that their ancestors like most Recent mygalo-

morphs were also burrowing spiders. As for the ctenizoids (and their closest relatives), the rather large chelicerae are observed in females, known for their higher burrowing activity. Hence, there are grounds to connect the observed enlargement of the chelicerae in the ctenizoid mygalomorph spiders to their further adaptations to their burrowing mode of life.

Separate attention should be paid to the short chelicerae of migids and some actinopodids considered by Kraus & Kraus [1993] as plagi axial, and thus closest to the type that



Figs 22–25. Chelicerae of higher mygalomorphs, prolateral view: 22 — *Anemesia* sp., Cyrtaucheniidae; 23 — *Cteniza* sp., Ctenizidae; 24 — *Damarchus* sp., Nemesiidae; 25 — *Chaetopelma* sp., Theraphosidae.

Рис. 22–25. Хелицеры высших мигаломорфов, пролатерально: 22 — *Anemesia* sp., Cyrtaucheniidae; 23 — *Cteniza* sp., Ctenizidae; 24 — *Damarchus* sp., Nemesiidae; 25 — *Chaetopelma* sp., Theraphosidae.

hypothetically could be ancestral for spiders. The problem which appears within the framework of this hypothesis lies in the fact that the mentioned taxa do not belong certainly to a number of the most primitive members even within their own group (Rastelloidina). For instance, the Migidae are characterized by the secondary loss of the cheliceral rastellum. Besides, according to Raven's [1985] opinion, a very characteristic eye arrangement in the form of a wide trapezium shared by the representatives of both families, is also a second apomorphic acquisition.

In contrast, the true archaic mygalomorphs, 'atypoids', possess well-developed orthognathous chelicerae. Palaeontological evidence shows that this type was shared by the known Mesozoic mygalomorph spiders [see Eskov & Zonstein, 1990b; Selden & Gall, 1992; Dunlop, 1993]. Taking this into consideration, the presence of short chelicerae in some mygalomorph taxa could be more preferably considered as a secondary apomorphic innovation rather than a plesiomorphy.

Some characters show closer resemblance between the liphistiid and mygalomorph or-

thognathous chelicerae. Symptomatically, even when considered in detail, the shape of the liphistiid chelicerae appears to be very similar to that in the Atypidae and, to a lesser degree, to the configuration of the chelicerae observed in two other families of so called 'atypoid' mygalomorphs. The grounds for drawing these parallels are as follows.

Firstly, in this case the fang attachment point seems not to be displaced completely on the ventral cheliceral surface (cf. Figs 18–21 vs. Figs 22–25). Secondly, both the Liphistiidae and 'atypoid' mygalomorphs possess a sharp dorsal cheliceral hook separating a swollen dorsal lobe from the cheliceral base⁵, whereas in other mygalomorphs it is developed considerably less, or is almost completely absent (see the same figures)⁶. The last pair of characters was interpreted by Eskov & Zonstein [1990b] as an autapomorphy of the 'atypoids' and a symplesiomorphy of the mygalomorphs, respectively. However, the presence of a very similar cheliceral hook in the Liphistiidae either makes their hypothesis doubtful or at least implies a homoplasy.

Raven [1985] gave five apomorphies in order to support mygalomorph monophyly: the completely reduced anterior median spinnerets; the subsegmented basal joint of the posterior lateral spinnerets; the anterior lateral spinnerets are much smaller than the posterior lateral ones; both the transverse duct of the posterior lungs and the apodemes are reduced entirely; the reduced number of the cardiomerer — four instead of five in the liphistiids. The peculiar form of the mygalomorph chelicerae representing a further modification of the neognathous mesothele type could be added to these apomorphies irrespective of the viewpoints considered here.

Araneomorphae

As noted above, the plagi axial chelicerae of *Hypochilus* and their affinities differ noticeably from the orthognathous construction in the li-

phistiids (Fig. 26). They only formally resemble the short-orthognathous chelicerae of some Actinopodidae, Migidae and Idiopidae: in spite of the fangs intersected at 90°, the latter possess basal cheliceral segments that are flattened pro-laterally and retain the primary longitudinal orientation (Figs 27, 28), typical for mygalomorphs. In contrast to the Hypochiloidea, their chelicerae are not directed downward and sideways [see Platnick & Shadab, 1976; Raven, 1984b; Goloboff & Platnick, 1987; etc]. However, the divergent hypochiloid chelicerae could be easily derived from the cheliceral construction of *Attercopus*, which almost ideally conforms to the role of the missing link between two main lineages in the development of spider chelicerae. Furthermore, the hypochiloid condition taken in itself appears to be an intermediate that could join the primary neognathous type of *Attercopus* and diaxial chelicerae of the higher araneomorphs. The first and the last variants are connected through the continuous chain of intermediates (as shown in Figs 29–31). It should be added that both those types coexisted at least since the early Mesozoic because the more advanced diaxial construction existed in the Triassic; later the latter type was widely distributed within the Mesozoic araneomorphs [see Eskov, 1984, 1987; Selden, 1990, 2001; Selden & Dunlop, 1998; Selden *et al.*, 1999].

It is most likely that the plagi axial model underlay the development of all the types of diaxiality. The so-called paralabidognathous chelicerae of the Filistatidae derived from the orthognathous state by Eskov & Zonstein [1990a], showed on more careful examination a doubtless resemblance to the cheliceral construction of the hypochilids (cf. Figs 32 and 33). This fact contradicts the concept of Eskov & Zonstein [1990a] supporting the separate evolution of the labidognathous filistatid chelicerae.

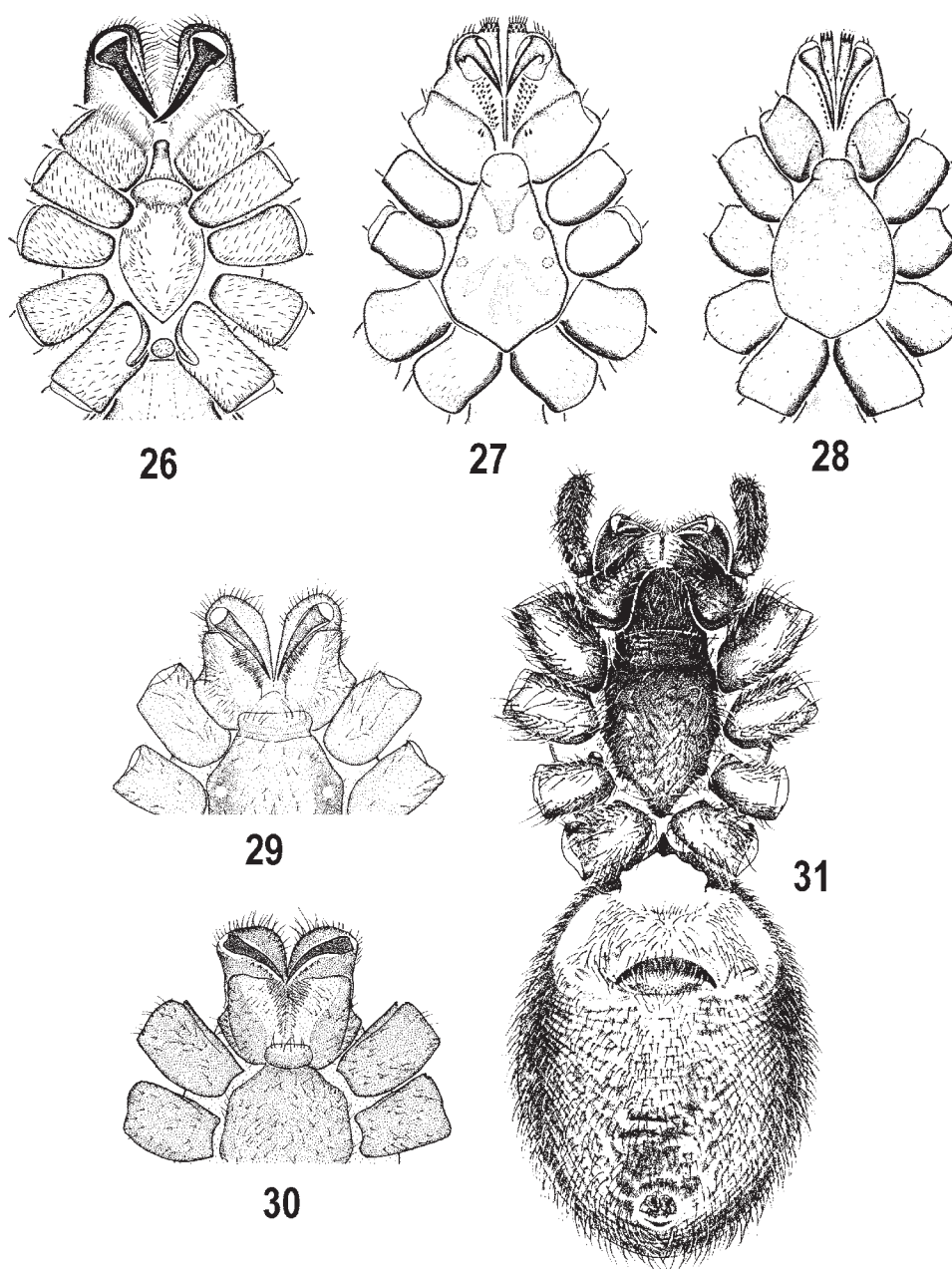
Evolution

Possible evolutionary factors

It is most likely that an improved web-building activity connected with feeding on flying and saltatory insects was the main factor that induced the origin and further development of labidognathy in spiders [Starobogatov, 1985;

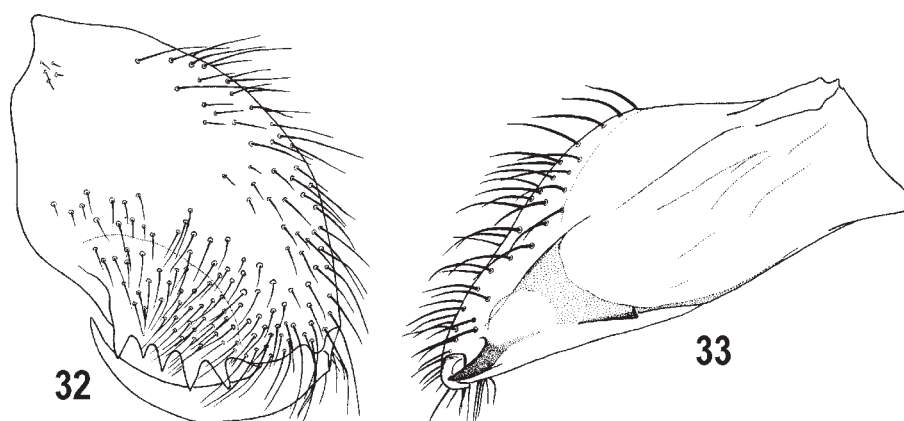
⁵ This cheliceral type was also figured by Coyle [1968, 1971, 1974] for Antrodiaetidae and by Gertsch & Platnick [1979, 1980] for Mecicobothriidae and Atypidae, respectively. The similar chelicerae of fossil Cretaceous mecicobothriids and antrodiaetids were described and figured by Eskov & Zonstein [1990b].

⁶ The few exceptions noted in passing by Eskov & Zonstein [Op.cit.: fig. 26d–f] do not contradict the general mode.



Figs 26–31. Principal cheliceral constructions in spiders, ventral view: 26 — *Liphistius* sp. [Platnick & Gertsch, 1976: fig. 5, modified]; 27 — mygalomorph *Neocteniza osa* Platnick et Shadab, female [Platnick & Shadab, 1976: fig. 7]; 28 — *Neocteniza fantastica* Platnick et Shadab, male [Op.cit.: fig. 8]; 29 — Hypochilidae; 30 — some Ctenidae; 31 — majority of araneomorph spiders (as a typical representative, the diguetid *Segestrioides bicolor* Keyserling is shown according to Platnick [1989: fig. 8]).

Рис. 26–31. Основные типы конструкции хелицер у пауков, вентрально: 26 — *Liphistius* sp. [Platnick & Gertsch, 1976: fig. 5, изменено]; 27 — mygalomorph *Neocteniza osa* Platnick et Shadab, самка [Platnick & Shadab, 1976: fig. 7]; 28 — *Neocteniza fantastica* Platnick et Shadab, самец [Op.cit.: fig. 8]; 29 — Hypochilidae; 30 — некоторые таксоны Ctenidae; 31 — большинство аранеоморфных пауков (в качестве типичного представителя этой группы приведена иллюстрация *Segestrioides bicolor* Keyserling, Diguetidae из Platnick [1989: fig. 8]).



Figs 32–33. Chelicerae of primitive araneomorph spiders, prolateral view: 32 — *Hypochilus coylei* Platnick, Hypochilidae; 33 — *Filistata insidiatrix* (Forskål), Filistatidae.

Рис. 32–33. Хелицеры примитивных аранеоморфов, пролатерально: 32 — *Hypochilus coylei* Platnick, Hypochilidae; 33 — *Filistata insidiatrix* (Forskål), Filistatidae.

Kraus & Kraus, 1993]. Due to the improvement of spider webs, efficient prey fixation in the araneomorphs became more dependent on utilizing the web. This very reason, perhaps, caused the further evolution of the diminished semi- to fully diaxial chelicerae characteristic for the Araneomorphae. However, the factors which caused the appearance of the highly-modified chelicerae in the ancestors of both the Mesothelae and the Mygalomorphae remain obscure and somewhat controversial.

Starobogatov [1985] connected the development of large orthognathous chelicerae with feeding by the orthognath spider ancestors on crustaceans and other armored arthropods. He suggested that “the paraxial chelicerae are undoubtedly more convenient when the prey should be shredded (because either it is too large, or it is defended by a shell); otherwise, the diaxial construction is more opportune when the prey is captured and squeezed close to the mouth. It looks reasonable that the paraxial chelicerae have been yet formed in those spiders, for which the insects were not a principal food source, but diaxial chelicerae were acquired in view of a transition to feeding exclusively on the insects” [Op.cit.: p. 8]. Unfortunately, this assumption cannot be either confirmed or disproved. None of the more reliable characters supporting the given trophic specialization of the orthognath spider ancestors can be observed in the palaeontological material.

According to Kraus & Kraus [1993], the development of orthognathy could be connected to a specific method of prey capture, when the prey is captured by spiders near the ground surface. This hypothesis appears to be better founded. Most taxa belonging to the Trigonotarbida actually possessed downward-directed orthognath chelicerae [see Shear *et al.*, 1987: fig. 54]. It should be noted, however, that this type of cheliceral modification was connected probably to the development of the ‘incapsulated’ state of the cephalothorax provided with a hypertrophied clypeus [Op.cit.: fig. 55]. Observations on the hunting mygalomorph spiders show that they do not attempt to clutch the captured prey to the ground surface. In contrast, they often try to raise the all too active victim upwards, thus decreasing its ability to resist.

None of the other arachnids possess paraxial chelicerae of similar shape. Hence, to explain the factors which caused the appearance of these modifications, one needs to focus rather on those features which are shared at least by most of the orthognath spiders; they also should be absent or at least underdeveloped within other orthognath arachnids. The only character corresponding to both above conditions is probably the burrowing activity common to the majority of spiders possessing the paraxial chelicerae.

Compared to the labidognathous chelicerae, the orthognathous construction shows lower efficiency, as was noted by Kaestner [1956].

This inefficiency could indicate that the shape of the spider orthognathous chelicerae actually represents an evolutionary compromise resulting from two competing functions of the same structure caused by burrowing and hunting activities. From this point of view, the configuration of the spider paraxial chelicerae seems to be rather suitable to unite both these functions.

The lower diversity of cheliceral forms within the orthognath spiders probably testifies in favour of the assumption that they became burrowers in the early stages of their evolution, i.e., their adaptive radiation took place after the orthognath spider chelicerae had been modified. The presence of forward-directed neognathous chelicerae in ancestral orthognath spiders could be considered the necessary preadaptation for the specific but narrow radiation of these groups.

Some evolutionary aspects

It is considered that the chelicerae of the tetrapulmonates arose from the three-segmented chelate type of the lower arachnids [Dunlop, 1997]; such a generalized precursor is shown in Fig. 34a. The cheliceral structures of *Amblypygi* and *Uropygi s.lat.*, where the majority of characters appear to have an intermediate position between two opposite states found in spiders and most primitive arachnids, are regarded here as transitional variants that could represent a base for further cheliceral evolution (Fig. 34b,c). Contrary to Dunlop [1997], in this study the trigonotarbid chelicerae are supposed to have been further modified to represent a direct precursor of the spider chelicerae (see above). It should be added that in orthognath spiders the fang insertion point seems to be displaced ventrad through disproportional development of upper and lower portions of the basal cheliceral segment. Seemingly, in trigonotarbids a similar configuration was achieved mainly because their axial orientation had been changed (Fig. 34d,e). Their resemblance to the cheliceral configuration in spiders could represent homoplasy.

The traditional viewpoint appears to be quite correct in treating the mygalomorph chelicerae as derived from the orthognathous mesothele type. In this case, the cheliceral constructions which occurred in the lower mygalomorphs allow us to consider them the halfway variants.

But the further evolution of the spider chelicerae suggested by this hypothesis looks improbable since it considers the distinctly modified chelicerae of the mygalomorphs as a precursor for the labidognathous type. One must agree with the opinion of Kraus & Kraus [1993] regarding the mygalomorph and araneomorph chelicerae as developed separately from each other. In principle, the peculiar form of the latter could be explained by a reverse of the basic phrynid configuration though redirected out- and downwards. But contrary to that, it could represent only a quasi-similar innovation developed through modification of the plagi axial type.

In its part, the latter hypothesis does not yet contradict the traditional spider classification because it places the chelicerae of the liphistiids into the plagi axial type; thus it assumes that the origin of the orthognathous and labidognathous variants took place when the suborder Opisthothelae was split into the corresponding infraorders. However, as stated above, the chelicerae of the Recent Liphistiidae cannot be referred to the same type that includes the plagi axial construction of the Hypochilidae. Judging from the fossils of *Paleothele*, the cheliceral variant of *Hypochilus* and those of fossil Paleozoic mesothele spiders were also dissimilar.

The cheliceral configuration found in the Devonian *Attercopus* (Fig. 34f) represents possibly the only version that appears suitable to be a prototype for all the Recent spider groups. Following this assumption, one can describe, consistently and without reversals, the further evolution of chelicerae in the main groups of the Araneae: the reinforcement of paraxial chelicerae in mesothele spiders (Fig. 34g) and their supplementary modification in the mygalomorphs (Fig. 34h,i); the origin of paraxial chelicerae in the hypochiloid spiders (Fig. 34j) and their gradual modification into the diaxial cheliceral construction of the more advanced araneomorph spiders (Fig. 34k). Although for *Attercopus* too little is known to conclude anything sufficient concerning its relationships, this taxon was a derivative of the primary spider group that gave rise to the liphistiids [both taxa share similarly shaped spigots; Selden *et al.*, 1991] and probably to all other spiders. Hence, based on the above-mentioned data, the mygalomorph and

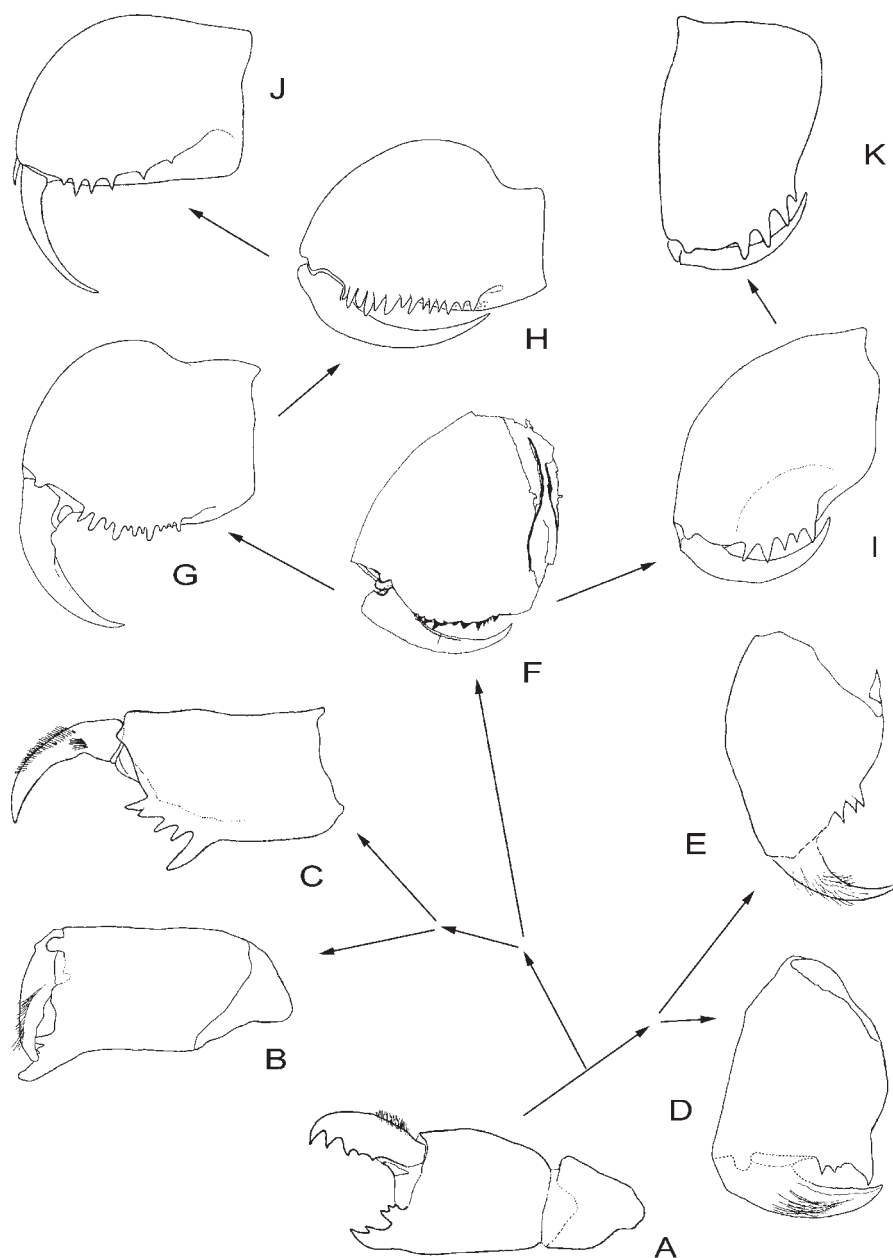


Fig. 34. Presumed evolution of chelicerae in main lineages of tetrapulmonate arachnids (with comments in the text): A — lower arachnids (Scorpiones — according to Stockwell, 1996, modified); B — schizomid *Stenochrus* [Tourinho & Kury, 1999, fig. 5]; C — whip spider *Charinus* [Giupponi & Kury, 2002: fig. 2]; D — some Trigonotarbida [Dunlop, 1997: fig. 4a]; E — trigonotarbid *Gelasinotarbus reticulatus* [Shear *et al.*, 1987, fig. 68]; F — *Attercopus* [Selden *et al.*, 1991: fig. 4c]; G — *Liphistius*; H — mecicobothriid *Megahexura* [Gertsch & Platnick, 1979: fig. 56, modified]; I — *Hypochilus*; J — nemesiid *Nemesia* [Loksa, 1966: fig. 1h, modified]; K — majority of Araneomorphae.

Fig. 34. Предполагаемая эволюция хелицер в главных группах Тетрапульмоната (комментарии приведены в тексте): A — низшие арахниды (Scorpiones — по Stockwell, 1996, изменено); B — схизомид *Stenochrus* [Tourinho & Kury, 1999: fig. 5]; C — фрин *Charinus* [Giupponi & Kury, 2002: fig. 2]; D — некоторые таксоны Trigonotarbida [Dunlop, 1997: fig. 4a]; E — тригонотарбид *Gelasinotarbus reticulatus* [Shear *et al.*, 1987: fig. 68]; F — *Attercopus* [Selden *et al.*, 1991: fig. 4c]; G — *Liphistius*; H — мещикоботриид *Megahexura* [Gertsch & Platnick, 1979: fig. 56, изменено]; I — *Hypochilus*; J — немезиид *Nemesia* [Loksa, 1966: fig. 1h, изменено]; K — большинство таксонов Araneomorphae.

Summary of character patterns of the variants considered.

Table.

Суммированные паттерны признаков всех рассмотренных вариантов.

Таблица.

Character	Traditional concept	Kraus & Kraus [1993]	This study
Primary cheliceral type within the Araneae	paraxial chelicerae	plagi axial chelicerae	paraxial chelicerae
Chelicerae of the Amblypygi	ancestral or close to basic type	arose independently from the Araneae	ancestral or close to basic type
Chelicerae of the Mesothelae	plesiomorphically orthognathous	close to plagi axial type	orthognathous but modified (neognathous)
Chelicerae of the Mygalomorphae	plesiomorphically orthognathous	represent further modification of the mesothele type	represent further modification of the mesothele type
Chelicerae of the Araneomorphae	arose through orthognathous type	arose independently from orthognathous type	arose independently from orthognathous type
Fang insertion point in the Mesothelae and the Mygalomorphae	[not specified]	unmodified	displaced ventrad
Axial orientation in the Mygalomorphae	unmodified	modified partially from plagi axial to paraxial type	modified partially from paraxial to plagi axial type
Plesiomorphic state of cheliceral furrow and fang in the Mygalomorphae	long furrow and fang	short furrow and fang	long furrow and fang
Cheliceral modifications in orthognath spiders result from:	peculiarities of feeding [Starobogatov, 1985]	peculiarities of prey capture	burrowing activity

araneomorph spiders might not be sister groups, though it is the conventional hypothesis.

On the other hand, the liphistiomorph and mygalomorph spiders could have acquired their cheliceral type independently from each other. It should be noted that both groups are represented mainly by burrowing forms with a restricted area of potential modifications. Therefore, such modifications should have been substantially narrower in scope than those seen in the araneomorphs. Such a concept appears to be more parsimonious since it eliminates the problem of multiple parallel reductions in the Mygalomorphae and the Araneomorphae required by the first hypothesis. However, the great similarity existing between cheliceral configurations in the liphistiids and the most archaic mygalomorphs in the framework of this variant remains unexplained.

Conclusions

1. The traditional concept treating the cheliceral construction in the orthognathous spiders as an initial state of the labidognathous cheli-

cerae is questioned. This hypothesis seems to have overlooked the fact that the described variants of chelicerae both in the Mesothelae and in the Mygalomorphae differ considerably from the hypothesized ancestral state.

2. The new approach first shown by Kraus & Kraus [1993] appears considerably more suitable to explain parsimoniously the origin and evolution of labidognathous chelicerae. Immediately, the hypothesis faces difficulties when it derives the orthognathous chelicerae from the hypothetical intermediate type, common with the labidognaths. The facts contradicting this hypothesis are as follows: (1) the most archaic mygalomorphs possess concurrently well-developed orthognathous chelicerae; (2) chelicerae of the Liphistiidae also differ noticeably from the assumed ancestral type; (3) the latter was not found in the pre-Cenozoic mesothele and mygalomorph fossils discovered in the last 15 years; like their Recent relatives, these forms also possessed paraxial chelicerae.

3. In the hypothesis proposed here the chelicerae both of the Liphistiidae and the Mygalo-

morphae can be treated as plesiomorphic by their position and axial orientation, but as apomorphic by their configuration; the latter seems to be an evolutionary compromise caused by burrowing activity. Whether the shared type in the above groups is a synapomorphy or a homoplasy remains uncertain although the cheliceral construction of archaic mygalomorphs shows some resemblance to that of liphistiids. In contrast, the cheliceral position in the Araneomorphae seems to be a definite autapomorphy, yet their configuration being much closer (as compared to the above mentioned groups) to that in the other tetrapulmonate orders should be considered either a symplesiomorphy or a reversal. The distinctions occurred between the traditional approach, Kraus & Kraus hypothesis of 1993, and the new version proposed in this study, are summarized in the Table.

4. The observed data generally support the Kraus & Kraus [1993] hypothesis, namely that the two main cheliceral types arose independently of one another. Unlike the cheliceral construction which occurred in other orders of the Tetrapulmonata, paraxial chelicerae of the Recent orthognath spiders are modified to such an extent that they cannot represent the basic construction for the Araneomorphae.

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References

- Bristowe W.S. 1933. The liphistiid spiders. With an appendix on their internal anatomy by J. Millot // Proc. Zool. Soc. Lond. Vol.103. P.1016–1057.
- Coyle F.A. 1968. The mygalomorph spider genus *Atypoides* (Araneae, Antrodiaetidae) // Psyche. Vol.75. P.157–194.
- Coyle F.A. 1971. Systematics and natural history of the mygalomorph spider genus *Antrodiaetus* and related genera (Araneae, Antrodiaetidae) // Bull. Mus. Comp. Zool. Harv. Vol. 141. P.269–402.
- Coyle F.A. 1974. Systematics of the trapdoor spider genus *Aliatypus* (Araneae, Antrodiaetidae) // Psyche. Vol. 81. P.431–500.
- Coyle F.A. 1981. The mygalomorph spider genus *Microhexura* (Araneae, Dipluridae) // Bull. Am. Mus. Nat. Hist. Vol. 170. P.64–75.
- Coyle F.A. 1986. *Chilehexops*, a new funnelweb mygalomorph spider genus from Chile (Araneae, Dipluridae) // Am. Mus. Novit. No.2860. P.1–10.
- Coyle F.A. 1988. A revision of the American funnel-web mygalomorph spider genus *Euagrus* (Araneae, Dipluridae) // Bull. Am. Mus. Nat. Hist. Vol.187. P.203–292.
- Dunlop J.A. 1993. A review of fossil mygalomorphs // Mygalomorph. Vol.1. P.1–17.
- Dunlop J.A. 1994. Filtration mechanisms in the mouthparts of tetrapulmonate arachnids // Bull. Br. Arachnol. Soc. Vol.9. No.8. P.605–614.
- Dunlop J.A. 1996a. A trigonotarbid arachnid from the Upper Silurian of Shropshire // Palaeontology. Vol.39. P.605–614.
- Dunlop J.A. 1996b. Systematics of the fossil arachnids // Rev. Suisse Zool. (Vol. Hors Série 2). P.173–184.
- Dunlop J.A. 1996c. Evidence for a sister group relationship between Ricinulei and Trigonotarbida // Bull. Br. Arachnol. Soc. Vol.10. No.6. P.193–204.
- Dunlop J.A. 1997. Paleozoic arachnids and their significance for arachnid phylogeny // Żabka M. (ed.) Proc. 16th Europ. Coll. Arachnol., Siedlce, Poland. P.65–82.
- Eskov K.Yu. 1984. A new fossil spider family from the Jurassic of Transbaikalia (Araneae: Chelicerata) // Neues Jahrbuch Geol. Paläontol., Monatshefte. Hft. 1984. S.645–653.
- Eskov K.Yu. 1987. A new archaetid spider (Chelicerata: Araneae) from the Jurassic of Kazakhstan, with notes on the so-called 'Gondwanan' ranges of recent taxa // Neues Jahrbuch Geol. Paläontol. Abhandl. Bd.175. Hft.1. S.81–106.
- Eskov K.Yu. & Zonstein S.L. 1990a. A new classification for the order Araneida (Arachnida: Chelicerata) // Acta Zool. Fenn. Vol.190. P.129–137.
- Eskov K.Yu. & Zonstein S.L. 1990b. First Mesozoic mygalomorph spiders from lower Cretaceous of Siberia and Mongolia, with notes on the system and evolution of the infraorder Mygalomorphae // Neues Jahrbuch Geol. Paläontol. Abhandl. Bd.178. Hft.3. S.325–368.
- Gertsch W.J. & Platnick N.I. 1979. A revision of the spider family Mecicobothriidae (Araneae, Mygalomorphae) // Am. Mus. Novit. No.2687. P.1–32.

- Gertsch W.J. & Platnick N.I. 1980. A revision of the American spiders of the family Atypidae (Araneae, Mygalomorphae) // *Am. Mus. Novit.* No.2707. P.1–39.
- Giribet G., Edgecombe G.D., Wheeler W.C. & Babbitt C. 2002. Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data // *Cladistics.* Vol.18. P.5–70.
- Giupponi A.P. & Kury A.B. 2002. A new species of *Charinus* Simon, 1892 from northeastern Brazil (Arachnida, Amblypygi, Charinidae) // *Bol. Mus. Nac. Zool. Rio.* No.477. P.1–7.
- Goloboff P.A. & Platnick N.I. 1987. A review of the Chilean spiders of the superfamily Migoidea (Araneae, Mygalomorphae) // *Am. Mus. Novit.* No.2888. P.1–15.
- Grasshoff M. 1978. A model of the evolution of the main chelicerate groups // *Symp. Zool. Soc. Lond.* No.42. P.273–284.
- Harvey M.C. 2002. The neglected cousins: what we do know about the smaller arachnid orders? // *J. Arachnol.* Vol.30. P.357–372.
- Harvey M.C. 2003. Catalog of the smaller arachnid orders of the world. Amblypygi, Uropygi, Schizomida, Palpigradi, Ricinulei and Solifugae. CSIRO Publ. 400 p.
- Kaestner A. 1956. Lehrbuch der speziellen Zoologie. Wirbellose. Bd.1. Hft.5. S.485–658.
- Kraus O. & Kraus M. 1993. Divergent transformation of chelicerae and original arrangement of eyes in spiders (Arachnida, Araneae) // *Mem. Queensland Mus.* Vol.33. No.2. P.579–584.
- Loksa I. 1966. *Nemesia pannonica* O. Herman (Araneae, Ctenizidae) // *Ann. Univ. Sci. Budap. Sect. Biol.* Vol.8. P.155–171.
- Mikhailov K.G. 1992. Third Eurasian Arachnological Conference // *Arthropoda Sel.* Vol.1. No.3. P.99–100.
- Miller J.A. 2003. Assessing progress in systematics with continuous jackknife function analysis // *Syst. Biol.* Vol.52. No.1. P.55–65.
- Ono H. 1999. Spiders of the genus *Heptathela* (Araneae, Liphistiidae) from Vietnam, with notes on their natural history // *J. Arachnol.* Vol.27. P.37–43.
- Palmer J.M. 1985. The silk and silk production system of the funnel-web mygalomorph spider genus *Euagrus* (Araneae, Dipluridae) // *J. Morph.* Vol.186. P.195–207.
- Platnick N.I. 1989. A revision of the spider genus *Segestrioides* (Araneae, Diguettidae) // *Am. Mus. Novit.* No.2940. P.1–9.
- Platnick N.I. & Gertsch W.J. 1976. The suborders of spiders: a cladistic analysis (Arachnida, Araneae) // *Am. Mus. Novit.* No.2607. P.1–15.
- Platnick N.I. & Sedgwick W.C. 1984. A revision of the spider genus *Liphistiis* (Araneae, Mesothelae) // *Am. Mus. Novit.* No.2781. P.1–31.
- Platnick N.I. & Shadab M.U. 1976. A revision of the mygalomorph spider genus *Neocteniza* (Araneae, Actinopodidae) // *Am. Mus. Novit.* No.2603. P.1–19.
- Pocock R.I. 1893. On some point in the morphology of the Arachnida (*s.str.*) with some notes on the classification of the group // *Ann. Mag. Nat. Hist. Ser.6.* No.11. P.1–19.
- Raven R.J. 1984a. Systematics of the Australian curtain-web spiders (Ischnothelinae: Dipluridae: Chelicerata) // *Aust. J. Zool. Suppl. Ser.* Vol.93 P.1–102.
- Raven R.J. 1984b. Systematics and biogeography of the mygalomorph spider family Migidae (Araneae) in Australia // *Aust. J. Zool.* Vol.32 P.379–390.
- Raven R.J. 1985. The spider infraorder Mygalomorphae (Araneae): Cladistics and systematics // *Bull. Amer. Mus. Nat. Hist.* Vol.182. P.1–180.
- Selden P.A. 1990. Lower Cretaceous spiders from the Sierra de Montsech, north-east Spain // *Palaeontology.* Vol.33. P.257–285.
- Selden P.A. 1996a. First fossil mesothele spider from the Carboniferous of France // *Rev. Suisse Zool.* (Vol. Hors Série 2). P.585–596.
- Selden P.A. 1996b. Fossil mesothele spiders // *Nature.* Vol.379. P.498–499.
- Selden P.A. 2000. *Paleothele*, replacement name for the fossil mesothele spider *Eothele* Selden *non* Rowell // *Bull. Br. Arachnol. Soc.* Vol.11. P.272.
- Selden P.A. 2001. Eocene spiders from the Isle of Wight with preserved respiratory structures // *Palaeontology.* Vol.39. P.583–604.
- Selden P.A. & Dunlop J.A. 1998. Fossil taxa and relationships of chelicerates // Edgecombe G.D. (ed.). *Arthropod fossils and phylogeny.* New-York: Columbia Univ. Press. P.303–331.
- Selden P.A. & Gall J.-C. 1992. A Triassic mygalomorph spider from the northern Vosges, France // *Palaeontology.* Vol.35. P.211–235.
- Selden P.A., Shear W.A. & Bonamo P.M. 1991. A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Araneae // *Palaeontology.* Vol.34. P.241–281.
- Selden P.A., Anderson J.M., Anderson H.M. & Fraser N.C. 1999. Fossil araneomorph spiders from the Triassic of South Africa and Virginia // *J. Arachnol.* Vol.27. P.401–414.
- Shear W.A., Selden P.A., Rolfe W.D.I., Bonano P.M. & Grierson J.D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida) // *Am. Mus. Novit.* No.2901. P.1–74.
- Shultz J.W. 1990. Evolutionary morphology and phylogeny of Araneida // *Cladistics.* Vol.6. P.1–38.
- Shultz J.W. 1999. Muscular anatomy of a whip spider, *Phrynus longipes* (Pocock) (Arachnida, Amblypygi), and its evolutionary significance // *Zool. J. Linn. Soc.* Vol.126. P.81–116.
- Starobogatov Ya.I. 1985. [The taxonomic position and system of the spiders] // Ovtsharenko V.I. (ed.). *Fauna i ekologiya paukov SSSR.* Trudy Zool. Inst. AN SSSR. Vol.139. P.4–16 [in Russian, with English summary].
- Stockwell S. 1996. Scorpion terminology and morphology, online at <http://wrbu.si.edu/www/stockwell/morphology/morphology.html>
- Tourinho A.L.M. & Kury A.B. 1999. The southernmost record of Schizomida in South America, first records of Schizomida or Rio de Janeiro and of *Stenochrus* Chamberlin, 1922 for Brazil (Arachnida, Schizomida, Hubbardiidae) // *Bol. Mus. Nac. Zool. Rio.* No.405. P.1–6.
- Weygoldt P. & Paulus H.F. 1979. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. II. Cladogramme und die Entfaltung der Chelicerata // *Z. Zool. Syst. Evolutionsforschung.* Bd.17. S.177–200.
- Wheeler W.C. & Hayashi C.Y. 1998. The phylogeny of extant chelicerate orders // *Cladistics.* Vol.14. P.173–192.