BULLETIN DE L'INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE, SCIENCES DE LA TERRE, 57: 139-147, 1987
BULLETIN VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN, AARDWETENSCHAPPEN, 57: 139-147, 1987

Re-examination of the *castanea* versus *hippocastanea* problem in the District of Mackenzie, and establishment of a new early-middle Givetian rhynchonellid genus

by Paul SARTENAER

Abstract

Two Givetian species from the District of Mackenzie are examined: *Rhynchonella castanea* MEEK, 1867, of early Givetian age, which is chosen as the type species of a new early-middle Givetian genus, *Eliorhynchus,* and *Caryorhynchus hippocastanea* CRICKMAY, 1960 of late Givetian age. Conflicting views of the past on the more or less restricted understanding of the former species, and on the acceptance of the latter as a valid species, are briefly outlined. Some problems related to the genus *Ypsilorhynchus* SARTENAER, 1970 are considered. The necessity for a discussion of the historical, systematic and stratigraphical aspects of these taxa became evident during the study of the rhynchonellids described in a forthcoming paper by NORRIS, UYENO and SARTENAER on the brachiopods and conodonts of the middle Givetian Bituminous limestone member of the Pine Point Formation, on the south side of the Great Slave Lake.
Key-words: *Eliorhynchus* - Rhynchonellid - early-middle Givetian - Western Canada.

Résumé

L'auteur examine deux espèces givetiennes du District du Mackenzie: *Rhynchonella castanea* MEEK, 1867, du début du Givetien, choisie comme espèce-type d'un genre nouveau, *Eliorhynchus,* du début et de la partie moyenne du Givetien, et *Caryorhynchus hippocastanea* CRICKMAY, 1960, de la fin du Givetien. Un bref exposé est fait sur les vues contradictoires quant à la compréhension plus ou moins restrictive de la première espèce et à la reconnaissance de la seconde comme espèce valide. Quelques considérations sont émises à propos du genre *Ypsilorhynchus* SARTENAER, 1960. La nécessité d'une discussion des aspects historique, systématique et stratigraphique de ces taxa s'est imposée au cours de l'étude de quelques Rhynchonellides, qui paraîtra sous peu dans un travail consacré par NORRIS, UYENO et SARTENAER à la description des Brachiopodes et des Conodontes du calcaire bitumineux d'âge Givetien moyen de la Formation de Pine Point sur la rive sud du Grand Lac des Esclaves.
Mots-clefs: *Eliorhynchus* - Rhynchonellide - Givetien Inférieur, Moyen - Ouest canadien.

I. - Introduction

When, twenty years ago, I started to deal with the problems connected with the genus *Leiorhynchus* HALL, 1860, some 150 species, subspecies and varieties were assigned to it and its given range was: Silurian to Pennsylvanian. Of course, the first step I took was to critically examine the type species. JOHNSON (1974, p. 55) has aptly summarized the then prevailing situation: "During the century following the proposal of the genus *Leiorhynchus* HALL a large number of species has been assigned to it, but little real understanding of *Leiorhynchus* was evident until SARTENAER (1961) redescribed and reillustrated the type species, *Leiorhynchus quadracostatus*". As a matter of fact, the stage of confusion was such that almost any mention of *Leiorhynchus* had to be considered as meaningless, and any comparison of a genus with *Leiorhynchus* as whimsical.

The unfortunate choice of the "Four-ribbed orthis (O. quadracostata)" VANUXEM, 1842 as the type species was primarily responsible for the confusion, and I have listed (1961, p. 963) its disadvantages. We can now accept that *Leiorhynchus quadracostatus* is better understood.

The second step to take was to reinvestigate the various taxa unduly assigned to the genus *Leiorhynchus.* Although well under way the job is only partly done, and a few problems remain unsolved or are unsatisfactorily cleared up. Among such problems are the following to which I have recently devoted more attention in relation to a forthcoming paper, by NORRIS, UYENO and SARTENAER, on the brachiopods and conodonts of the middle Givetian Bituminous limestone member of the Pine Point Formation, on the south side of the Great Slave Lake, District of Mackenzie. In this paper the following two problems are dealt with: ① the understanding of *Rhynchonella castanea* MEEK, 1867; this species has been included by most authors in the genus *Leiorhynchus,* but, for the last fourteen years, has been attributed by North American authors to *Ypsilorhynchus* SARTENAER, 1970; however, these workers consider *Ypsilorhynchus* a subgenus of *Leiorhynchus*; ② the validity, as a species, of *Caryorhynchus hippocastanea* CRICKMAY, 1960, which contains the name of the previous species; the separation of the two has not always been accepted. The problem of the systematic position of the Frasnian species still placed in the genus *Leiorhynchus* will be treated in a separate paper.

II. - *Rhynchonella castanea* MEEK, 1867 versus *Caryorhynchus hippocastanea* CRICKMAY, 1960

Rhynchonella castanea MEEK, 1867 being a species of long standing, it seems reasonable to assume that it is well known, especially because of the excellent state of preservation of the three primary types, and the new collections from the type locality and the type area. This is not the case and one should not mistake the many references to the species found in the literature for the knowledge of the species; various taxa are hidden under the numerous quotations of the last forty-five years. Consequently, comparisons with other species, or even with other genera, and in particular with *Caryorhynchus hippocastanea* CRICKMAY, 1960 are distorted at the outset. In order to illustrate this point it will suffice to give two examples of *Rhynchonella castanea* encompassing various taxa: McLAREN (1962, pp. 83-91), in his description of the species, included specimens from the type area as well as from other regions in the Northwest Territories, and from northeastern British Columbia, and also, as indicated by the synonymy, *Caryorhynchus hippocastanea* from the Northwest Territories, and *Rhynchonella castanea* from central Nevada described and figured by WALCOTT (1884, pp. 153-155, pl. XV, figs. 1, 1a, 4, 4a); JOHNSON (1970, p. 2097) is of the opinion that "Both large and small forms of *Leiorhynchus castanea* are known, and this was recognized at least as early as 1884 by WALCOTT as evidenced by his Plate 15, figures 1, 4". We know now that the small specimen (Pl. XV, figs. 1, 1a) figured by WALCOTT (1884) can be included with great probability in *Leiorhynchus (Leiorhynchus) sartenaeri* JOHNSON, 1974, and I consider the large specimen (Pl. XV, figs. 4, 4a) as not belonging to the Canadian species.

It is therefore not vain to briefly go over the views of those authors, who have paid special attention to these two species. The Lectotype of the former originates in the base (early Givetian) of the Hare Indian Formation (as we know now; no age other than Devonian and no stratigraphic information in MEEK's 1867 publication) on Carnwath River (Lockhart River in MEEK's 1867 publication) in the Lower Mackenzie River Valley in the Northwest Territories. The Holotype of the latter species occurs at the top (late Givetian) of the Ramparts Formation at the west end of Carcajou Ridge in the Middle Mackenzie River Valley in the Northwest Territories. Mention of the two species outside these areas are not dicussed in this paper, and will be only indirectly and accessorily alluded to.

After WHITEAVES (1898, p. 425) there is a break of about fifty years before *Leiorhynchus castanea* is mentioned again by COOPER (*in* COOPER *et al.*, 1942, p. 1784). WARREN (1944, p. 112), in a later study of *L. castanea,* discussed the forms from the Northwest Territories as well as those of Nevada, and clearly conveyed that there is more than one species "in the group of forms at present ascribed to it". In addition he stated that there are "end forms so entirely distinct that they should be recognized by at least varietal names", that the assignment to the genus *Leiorhynchus* HALL is doubtful, and, thus, that a new genus "may have to be erected". Later on, going further into detail, WARREN and STELCK recognized: three distinct forms of *L. castanea* (1949, p. 142); a large variety of *L. castanea* (1949, p. 142); *L.* cf. *castanea, L. castanea sensu lata* which "does not provide a restricted zone fossil", and *L. castanea sensu strictu* which "as described by Meek... from collections from Anderson (Lockhart) River... is very distinct and... appears to be confined to a definite horizon... has not been reported from areas outside of the Northwest Territories" (1950, p. 73); *Caryorhynchus castanea* var. (1956, pl. VIII, figs. 29-31, and WARREN, 1957, p. 2). Hence it appears that WARREN and STELCK from 1956 on, were content with *Caryorhynchus* CRICKMAY, 1952 being the new genus suspected by WARREN (1944, p. 112), although they later (1962, pp. 276-280, 282) came back to *Leiorhynchus,* as did CRICKMAY (1970, p. 73) after having accepted *Caryorhynchus castanea* in his publications between 1952 and 1967. During this period all other authors [with the exception of BASSETT and STOUT (1967, p. 738), who favoured *C. castanea*], including myself, have maintained the Canadian species in the genus *Leiorhynchus.*

The form BASSETT alluded to when he wrote "a similar but larger [than *'Nudirostra' castanea*] species of *'Nudirostra'*" (First International Symposium on Arctic Geology, held in Calgary, Alberta, January 11-13, 1960, published in 1961, p. 497, foot-note 6) is, in fact, nothing else than WARREN and STELCK's large variety. This large species becomes *Caryorhynchus hippocastanea* of CRICKMAY (1960, pp. 3, 13, 19); CRICKMAY forgets to mention BASSETT's statement, but JOHNSON (1978, p. 126) set his heart on rectifying this omission. WARREN and STELCK (1962, pp. 277, 278) did not accept this species and maintained that "The writers contend that this species is normally restricted to a mid portion of the Givetian Stage and that the form may be used as a time-stratigraphic marker"; "the authors have assumed that *Leiorhynchus hippocastanea* CRICKMAY is a local variant of *L. castanea* (MEEK), with the former probably confined to a later portion of the complete *L. castanea* 'range zone'". This is also the position of McLAREN (1962, pp. 83, 90, 104), who further, neither recognized the need to assign *L. castanea* to another genus than *Leiorhynchus,* nor the validity of the genus *Caryorhynchus*: "There is nothing in *Leiorhynchus castanea* to suggest generic difference from the type species of the genus", "None of the characters listed serve to distinguish *Caryorhynchus* from *Leiorhynchus* except the 'short dental lamellae'". As far as CRICKMAY (1963, pp. 7, 9) was concerned, he considered *Caryorhynchus castanea* as the possible ancestor of *C. hippocastanea,* and stated that "there is a great deal of difference in

external form between the two, and this is readily seen when the observer has plenty of good specimens of both". Yet, fully aware of the diversity of forms ascribed to *C. castanea,* CRICKMAY (1970, p. 73) was more explicit in stating that in his opinion there is only one "true *castanea*". JOHNSON's (1970, pp. 2091, 2097, 2098) attitude was quite different. On one hand, he makes *Leiorhynchus castanea* more encompassing: "large specimens of *L. castanea* are known", "both large and small forms of *L. castanea* are known", "large specimens of *L. castanea* which approach specimens of *L. hippocastanea* in size"*. On the other hand, he declared that the two species are "much alike externally", but very distinct when considering the "discrete dental plates" — CRICKMAY (1963, p. 9) had already declared them distinctive —, and the "spindle-shaped adductor impressions" of *L. hippocastanea.*

Consequently, at this stage, we have two opposite points of view at the specific level, and some wavering at the generic level:

1. - *castanea* and *hippocastanea* are one and the same species according to MCLAREN, STELCK and WARREN, but it belongs to the genus *Leiorhynchus* for the first author and to the genus *Caryorhynchus,* and then back to *Leiorhynchus,* for the two others;
2. - *castanea* and *hippocastanea* are different species for BASSETT, CRICKMAY, and JOHNSON, but they belong to the genus *Leiorhynchus* for the first and the third author, and to the genus *Caryorhynchus,* and then back to *Leiorhynchus,* for the second. Further, the external differences are important for the second author, while they are insignificant for the third author.

From 1973 (p. 469) forth JOHNSON takes a decided step in separating *Leiorhynchus (Leiorhynchus) hippocastanea* from *Leiorhynchus (Ypsilorhynchus) castanea* on the subgeneric level on account of the internal differences he mentioned in 1970. Since then these designations are in common use in the North American literature. I explain further my complete disagreement with the lowering of the genus *Ypsilorhynchus* to the rank of a subgenus, with its attribution to the genus *Leiorhynchus,* and with the assignment of *castanea* to it.

It is also time to put an end to this geologically and paleontologically unacceptable fiction of two strictly restricted stratigraphic markers: one at the very base [the *Eliorhynchus castanea* bed(s)], the other at the very top [the *Leiorhynchus hippocastanea* bed(s)] of the Givetian, almost without anything in between. We must accept that we are dealing with range zones of wider stratigraphic range, and that the small to medium sized *Eliorhynchus castanea* is also represented by larger specimens as well as the large *Leiorhynchus hippocastanea* by small to medium sized specimens. This variation in size is indicative of successive growth stages or/and of the evolution in time of these species. It is already demonstrable that small to medium sized specimens of *L. hippocastanea* are present not only in the coquina beds found in the upper 20 to 30 feet of the Ramparts Formation, but also as far down as 60 feet (GSC loc. 45391) below the top of this formation and large specimens are also to be found at 65 feet below the top of the same formation (GSC loc. 45395). Thus, the *L. hippocastanea* coquina represents the acme or the "blooming" of the species.

It seems that we are witnessing something similar with *L. quadracostatus.* This species exists in the upper eight feet of the Geneseo shale (= type horizon) and the lower five feet of the Sherburne flagstone in southwestern New York. The best specimens collected so far are of small size, but, small, medium and large size specimens are present on many slabs and represent, in all probability, the various growth stages. Nevertheless, some slabs carry specimens of the same size (usually of small or of medium size). It is therefore conceivable, although it still would have to be demonstrated — this is rendered difficult by the poor outcrop conditions —, that the specimens of small size are chiefly to be found in the oldest beds and correspond to the early stages of the species.

A concluding remark must be made on the possibility of regarding *L. hippocastanea* as a geographic variety of *L. quadracostatus.* JOHNSON (1970, p. 2100), thinking that the differences between the two species were "small and that there is some overlap in morphology", "considered suggesting that *L. hippocastanea* might best be regarded as a geographic subspecies of *L. quadracostatus,* but the nomenclature would be ponderous and probably not much would be gained". In 1979 (p. 296), referring to his previous publication, he wrote: *"Leiorhynchus quadracostatus,* which I consider to be (JOHNSON, 1970b) a geographical variant of *L. hippocastanea*". Although some differences are difficult to ascertain with certainty on account of the crushed, deformed and decalcified state of most specimens of *L. quadracostatus,* I believe that the different general costal formula (for *L. quadracostatus*: $\frac{4}{3}$; 0; 1 to 10; for *L. hippocastanea*: $\frac{5-9}{4-8}$; 0; 6 and more) alone allows one to maintain the southwestern New York and the central Mackenzie River Valley species as separate taxa. This is also the conservative approach adopted by JOHNSON.

*, It is not without interest to note that JOHNSON (1974, p. 56) considered Hypotype C of *L. castanea* chosen by MCLAREN (1962, p. 83, pl. XIV, figs. 4a-e) in the Anderson River valley as a "narrow variety", even though it was derived from the type area. This was already the position adopted by WALCOTT (1884, p. 154), who, commenting on MEEK's (1867) species from the Mackenzie River Basin, wrote: *"Rhynchonella castanea* is one of the variations of the species as it occurs in the Eureka District".

III. - Description of *Eliorhynchus* n. gen.

DERIVATIO NOMINIS

The name is formed by the inversion of the two first letters of the genus name *Leiorhynchus* in allusion to the fact that, until now, this form has been chiefly included in that genus.

TYPE SPECIES

Rhynchonella castanea MEEK, 1867.
The Lectotype (chosen by McLAREN, 1962, p. 83), adequately lithographed in the original publication, has been published anew (with magnification × 1.5) by JOHNSON (1974, pl. 3, figs. 1-5), but wrongly named Holotype. Other specimens from the type area have been photographed and serially sectioned by McLAREN (1962, fig. 22D *in textu* p. 78, fig. 24 *in textu* p. 86, Pl. XIV, figs. 2a-e, 3a-e, 4a-e, 5a-e). Further topotypical material has been illustrated in subsequent literature.
Following the majority of authors, I have always considered 1867 as the year of publication of part one of the first volume of the Transactions of the Chicago Academy of Sciences. It is the date indicated on the cover and it seems reasonable to accept that the printing was concluded that year. The distribution of the volume was delayed only to the very beginning of the year 1868 on account of unfortunate circumstances. As a matter of fact the editor writes, on February 4th 1868, on the first page of the book: "An apology is due to the contributors to this Part, for the delay in its appearance. This has been caused by the occurrence of certain unavoidable accidents". Only an historian or a jurist, probably both, could shed the most appropriate light on the formal aspects to be considered in dealing with such an exceptional case.
In restricting the investigated territory to the type area (Lower Mackenzie River Valley) and to the nearby region (Middle Mackenzie River valley), it can be stated that Canadian geologists, as far back as WARREN 1944, pp. 106-107, 112), have considered the bed(s) containing *Eliorhynchus castanea* as a distinctly recognizable unit, almost completely devoid of any other macrofauna. It is also WARREN (1944, p. 107) who introduced the "*Leiorhynchus castanea* fauna", while the "*Leiorhynchus castanea* zone" was used for the first time by WARREN and STELCK (1950, p. 62, fig. 1, p. 73). This unit, only a few metres thick, encompasses either the uppermost beds of the Hume Formation (previously lower Ramparts Formation), or the lowermost beds of the Hare Indian Formation (previously middle Ramparts Formation), or the transitional beds between the two formations, depending on the opinion of the authors concerning the boundary between these two lithostratigraphic units. From 1944 to 1962 these beds were considered of Upper Devonian age by WARREN, and by WARREN and STELCK. CRICKMAY (1960, pp. 2-3) and BASSETT (1961, p. 482, table I) gave them a mid Middle Devonian, and HOUSE and PEDDER (1963, p. 494, text-fig. 2) a middle Givetian age. Since BRAUN (1966, fig. 1), BASSETT and STOUT (1967, p. 738), NORRIS (1967, p. 756, fig. 3, p. 773), an early part of the Givetian, but never the base of the Givetian, is the widely accepted age, as it may be read in further publications by McLAREN, NORRIS and CUMMING (1970, p. 615, pl. XI-4), CALDWELL (1971, p. 20, text-fig. 2), etc... Meanwhile the beginning of the range of *Eliorhynchus castanea* was being investigated. First, BASSETT (1961, p. 489) mentioned the late Couvinian age on the basis of brachiopods, pelecypods, and corals. Then CHATTERTON (1976, p. 146) favoured an "either latest Eifelian or, more probably, early Givetian time" for the beds under discussion after examination of the conodont faunas and the macrofauna. This position was almost exactly restated by CHATTERTON (1978, p. 171, fig. 3, p. 177, fig. 4, p. 183), who wrote "the evidence available at present points to an early to middle Eifelian age for the lower part of the Hume Formation and a late Eifelian age for the top of this formation. An early Givetian age for the uppermost beds of the Hume Formation is, however, by no means impossible"; but, at the same time, this author pointed out that the top beds of the Hume Formation are contained in the Eifelian *Polygnathus pseudofoliatus* faunal unit. The same year, UYENO (1978, p. 237, fig. 2, p. 238), using conodont and cephalopod evidence, suggested an age older than the one of the *P. varcus* Zone for the oldest beds containing *Eliorhynchus castanea*; this means the *Polygnathus xylus ensensis* Zone without any possibility of deciding if the entire zone or only its upper part is involved. This line is now commonly followed (*see* PEDDER, 1982, p. 560, text-fig. 2; NORRIS, 1985, p. 4, 21, 29, 30, 49, figs. 3, 4).
In short, at this time, it cannot be demonstrated that the *Eliorhynchus castanea* Zone, considered here as a range zone, starts at the base or in the lower part of the *Polygnathus xylus ensensis* Zone in the type area and in the adjacent region. Therefore, and considering that this conodont zone straddles the Eifelian-Givetian boundary, it may be concluded that the *Eliorhynchus castanea* Zone is without any doubt of early Givetian age, and that a very late Eifelian age, although not proved, cannot be definitely dismissed for its lowermost part.

DESCRIPTION

Generally small to medium sized, exceptionally large. In cardinal view the contour is generally helmet-shaped (brachial valve) with check-strap (pedicle valve) still attached. Oval elliptical or rounded contour in ventral and dorsal views, slightly modified in a subpentagonal contour in ventral view. Strongly inequivalve, inflated, globulose. Dorsal umbonal

region always more or less strongly projected posteriorly beyond the pedicle valve. Cardinal line short and undulated. Postero-lateral margins concave near the commissure. Commissure sharp. Frontal and lateral commissures slightly undulated by the low costae, the lateral commissures sometimes not at all.

Contour of pedicle valve is a more or less regular half-ellipse in longitudinal median sections, a very flattened half-ellipse in transverse median sections. From a postero-median protuberance, the slope of the ventral flanks toward the lateral commissures increases progressively from slightly anteriorly to steeply posteriorly. Weakly developed sulcus, not easy to separate from the flanks where it starts, and only well marked at the junction of the frontal and lateral commissures, where it is low — two to three times the height of the low costae — and where it reaches its greatest width, which is noticeable (for *Eliorhynchus castanea*: 61 to 75 per cent of the width of the shell, most of the values varying from 64 to 69 per cent). Sulcus, with a flat to slightly convex bottom, starting at a great distance from the beak (for *E. castanea*: between 58 and 73 per cent, generally between 58 and 66 per cent, of the length of the shell or between 44 and 55 per cent of the unrolled length of the valve) with a width fluctuating around one third of the width of the shell (for *E. castanea*: varying from 27 to 35 per cent), and widening slowly. Tongue high with sharp borders, standing out clearly, usually trapezoidal. Upper part of the tongue only exceptionally vertical. The top of the tongue, which is at the most anterior point of the shell never coincides with the top of the shell (for *E. castanea*: located between 8 and 25 per cent, generally between 15 and 25 per cent, of the thickness of the shell from its top). Beak small, erect to slightly incurved, not overhanging the cardinal line, but nevertheless in contact or nearly in contact with the inflated dorsal umbo, resorbed by a small subcircular foramen. Ventral interarea short and generally concealed. Deltidial plates observed in transverse serial sections.

Curve of brachial valve, in longitudinal median sections, is one quarter of an ellipse slightly deformed by the inflation of the umbonal region. Helmet-shaped contour in cardinal view. Dorsal flanks steep, vertical or almost vertical near the lateral commissures. Fold with flat to slightly convex top, low to moderately high, beginning at a great distance from the beak, not easy to separate from the flanks where it starts, but well marked anteriorly.

Top of pedicle valve located posteriorly (for *E. castanea*: between 25 and 34 per cent of the length of the shell forward of the beak or between 21 and 29 per cent of the unrolled length of the valve). Greatest thickness of the brachial valve never at the front, but posterior (sometimes very posterior) to it (for *E. castanea*: located at a point between 34 and 68 per cent of the length of the shell posterior to the frontal commissure), and, from this point, the valve curves gently toward the commissure. Length measured between a plane tangent to the dorsal umbo and the top of the tongue. Length is the largest dimension. Greatest width around mid-length (for *E. castanea*: located at a point between 49 and 59 per cent of the length of the shell anterior of the ventral beak). Thickness and width may exceptionally be subequal (for *E. castanea*: t./w. ratios vary between 0.81 and 0.99, generally between 0.84 and 0.91). Apical angle wide (for *E. castanea*: from 103° to 120°, generally between 114° and 120°).

Very low costae, weakly marked although clearly visible, wide, rounded. Median costae beginning far from the beaks, more or less at level with the beginning of sulcus and fold (generally between one-third and one-half the unrolled length of the valves; sometimes may begin somewhat closer). Median costae wide at front (for *E. castanea*: usually between 1.5 and 2 mm, but may reach, exceptionally, 2.5 mm). The two following features account for median costae being commonly irregular: divisions (for *E. castanea*: observable in about fifty per cent of the specimens; usually one costa is divided, exceptionally two); in many specimens, the middle median costa (or one of the two middle median costae) is wider and higher than the others (this is the case for forty per cent of the specimens of *E. castanea,* including the Lectotype). When present, lateral costae are simple, regular, and restricted, with rare exceptions, to the anterior half of the shell, and even to the antero-lateral margins only; only the internal one(s) may reach mid-length, and the external one(s) are often almost inconspicuous. Number of costae moderate (for *E. castanea*: the general costal formula is $\frac{4–5}{3–4}$; 0; $\frac{2–6}{3–7}$).

No parietal costae. Fine growth lines often visible, especially in the anterior part of the shell.

Shell material thick.

Dental plates present, moderately stout, developed only in the extreme posterior part of the pedicle valve; they strongly converge anteriorly, and they join either before reaching the floor of the valve, or sometimes when they reach it. Well developed ventral umbonal cavities. Teeth small, short, slender and outwardly directed. Denticula well developed. The slightly impressed ventral muscle impressions form an oval area pointed posteriorly and rounded anteriorly. The width of the muscle field varies between 25 and 35 per cent the width of the shell, and its anterior end is located around mid-length of the shell. The small subcordiform to subreniform adductor scars are enclosed anteriorly by the larger flabelliform diductor scars.

Septum thin to blade-shaped dorso-anteriorly, thickened lensewise posteriorly, with a length that may extend as far as mid-length of the shell, but usually shorter. Hinge plate virtually non existing, marked in the middle by a low and narrow crural trough. Dental sockets narrow, low, short. Slender crural bases

passing progressively forward into relatively long and slender crura that curve ventrally at their distal ends; they are very near to each other in their proximal parts, and diverge progressively and slightly. Successive aspects of crura in transverse serial sections are oval-shaped and trough-shaped. Well marked elongate and lanceolate dorsal muscle field. The dorsal muscle scars are spindle-shaped — that is elongate and narrow — and may extend forward as far as mid-length of the shell. They are strongly impressed on each side of the septum, bounded by strong ridges; sometimes these ridges do not enclose the muscle scars completely, because they fade anteriorly before the scars do.

DIAGNOSTIC CHARACTERS

Small to medium sized. Helmet-shaped in cardinal view. Oval, elliptical or rounded in dorsal view. Strongly inequivalve. Dorsal umbonal region more or less strongly projected posteriorly beyond the pedicle valve. Sulcus and fold starting at relatively great distances from the beaks. Weakly developed sulcus, not easy to separate from the flanks where it starts. Top of the tongue located at the most anterior point of the shell. Greatest thickness posterior to the front. Length is the largest dimension. Moderate number of very low and weakly marked costae. Median costae beginning far from the beaks. Lateral costae starting far from the umbonal regions. Divisions occur in the median costae. Dental plates converging anteriorly, and then joining either before reaching the floor of the valve, or sometimes when they reach it. Septum thin to blade-shaped dorso-anteriorly, thickened lensewise posteriorly. Hinge plate virtually non-existing. Narrow crural trough.

COMPARISONS

It is evident that *Eliorhynchus* n. gen. and *Leiorhynchus* exhibit similar features, as, until now, *E. castanea* has almost exclusively been assigned to the latter genus.

Leiorhynchus and *Eliorhynchus* n. gen. have the following features in common: globulose, inflated, and strongly inequivalve aspect; dorsal umbonal region always more or less strongly projected posteriorly beyond the pedicle valve; ventral and dorsal views showing an oval, elliptical or rounded contour, slightly modified in a subpentagonal contour in ventral view; helmet-shaped in cardinal view; commissure (sharpness, undulation by costae); postero-median protuberance in the pedicle valve; slope of the ventral flanks; low and weakly developed sulcus with flat or slightly convex bottom; tongue (standing out clearly; its upper part only exceptionally vertical, and never recurved posteriorly; its top at the most anterior part of the shell which never coincides with the top of the shell); small erect to slightly incurved beak in contact or nearly in contact with the inflated brachial umbo; low to moderately high fold; greatest thickness of the brachial valve never at the front, but posterior to it; length being the largest dimension; length measured between a plane tangent to the dorsal umbo and the top of the tongue; similar apical angle; very low, weakly marked, rounded, wide costae; irregular, divided median costae; simple lateral costae, clearly weaker than the median costae; external lateral costae often almost inconspicuous; similar number of median costae; no parietal costae; short moderately thick to thick dental plates developed only in the extreme posterior part of the pedicle valve; well developed umbonal cavities; small and short teeth; long septum, thin dorso-anteriorly, thickened lensewise posteriorly; narrow crural trough; slender and relatively long crura very near to each other; the long, spindle-shaped, strongly impressed and ridge-bounded dorsal muscle scars).

Eliorhynchus n. gen may be separated by: size (size may be larger in *Leiorhynchus*); sulcus and fold not easy to separate from the flanks of the valves where they start (they are easier to separate in the genus *Leiorhynchus*), usually wider, and starting at a great distance from the beaks; flanks of the sulcus slightly steeper; higher tongue; greatest thickness commonly located more anteriorly; median and lateral costae beginning, respectively, far from the beaks and far from the umbonal regions; dental plates converging anteriorly, and joining either before reaching the floor of the valve, or, sometimes where they reach it (in the genus *Leiorhynchus,* dental plates are less convergent, and do not join before reaching the floor of the valve, which they reach farther apart; they are also commonly deformed by a swelling of their median part — e.g., *see* transverse serial sections 10 and 11 by CRICKMAY, 1963, pl. 2, p. 35); hinge plate virtually non existing; oval ventral muscle impressions (in the genus *Leiorhynchus* they are longer and narrower). Finally, there is no fundamental difference between the dorsal muscle scars, although sometimes the bounding ridges in the genus *Eliorhynchus* do not completely enclose the muscle scars anteriorly.

Eliorhynchus n. gen. resembles the late Eifelian (and, perhaps, early Givetian) genus *Ypsilorhynchus* in the following features: helmet-shaped contour in cardinal view; strongly inequivalve; uniplicate; inflated; globulose; dorsal umbonal region always more or less strongly projected posteriorly beyond the pedicle valve; commissure sharp; contour of both valves in longitudinal and transverse median sections; low sulcus with flat to slightly convex bottom; tongue high, usually trapezoidal, with sharp borders, standing out clearly, its upper part never recurved posteriorly; top of the tongue located at the most anterior point of the shell and never coinciding with the top of the shell; incurved ventral beak in contact or nearly in contact with the inflated dorsal umbo; dorsal flanks steep, vertical or almost vertical near the lateral

commissures; low to moderately high fold; location of the top of the pedicle valve and of the greatest width; greatest thickness of the brachial valve never at the front; costae wide, rounded; median costae irregular, sometimes divided; no parietal costae; shell material thick; teeth small, short, slender; dental plates strongly converging anteriorly; septum thin to blade shaped dorso-anteriorly, thickened lensewise posteriorly; dental sockets narrow, low, short; crura very near to each other in their proximal parts, diverging progressively and slightly, and curving ventrally at their distal ends.

However, many characters make *Ypsilorhynchus* distinct from *Eliorhynchus* n. gen.: contour, in ventral and dorsal views, less variable and, as a rule, more transverse; larger size; frontal commissure strongly undulated by the costae; ventral flanks more developed (wider) and nearly flat at postero-lateral margins; well developed and well marked sulcus and fold, starting at a short distance from the beaks; sulcus easy to separate from the flanks, wider absolutely (but not proportionally); fold curving more sharply toward the frontal commissure (this is due to the fact that the greatest thickness of the brachial valve is often located more posteriorly); width is almost always the largest dimension; wider apical angle and wider angle of the cardinal commissure; well marked costae, starting at a short distance from the beaks; median costae low (but not extremely low) somewhat less irregular; different general costal formula (for *Y. manetoe*: $\frac{5\text{–}8}{4\text{–}7}$; 0; $\frac{6\text{-}8}{7\text{-}9}$) indicating a shift towards a higher number of costae; shorter and relatively thinner dental plates forming a Y-shaped "spondylium" with a robust ventral septum, this Y-shaped "spondylium" is always present and always narrower than the "small cushion" which is sometimes observed in *Eliorhynchus* (*see* CRICKMAY, 1963, pl. 2, p. 35, fig. 21 under the name *Caryorhynchus castanea*); hinge plate somewhat more developed; crural trough somewhat wider and deeper. Not enough material of *Ypsilorhynchus manetoe* is available for allowing comparison between the muscle fields.

SPECIES ATTRIBUTED TO THE GENUS

The only accurate description of *Eliorhynchus castanea* is the original one by MEEK (1867); in the type area, the species is generally of small size, and often narrow. Allowing for wider geographic and stratigraphic distribution of the species, subsequent descriptions have unduly incorporated various taxa in it. Among them are two species from the middle Givetian Bituminous limestone member of the Pine Point Formation; one of them belongs to *Eliorhynchus* n. gen. This is not the only species, outside the type species, which must be attributed to *Eliorhynchus* n. gen., because there are other representatives of the genus amidst the forms identified under the name *Leiorhynchus castanea* and *Leiorhynchus (Ypsilorhynchus) castanea,* both in the southwestern part of the District of Mackenzie and in central Nevada.

IV. - Validity of the genus *Ypsilorhynchus*

In JOHNSON's (1974, p. 56) vehement criticism of my description of the genus *Ypsilorhynchus* there are elements which are linked to concepts. In this connection it is desirable that my position should be clearly understood.

According to me the *diagnosis* of a new genus is not restricted to one or two characters, but to a combination of various characters, which allows one to distinguish it from the group of nearly related genera, and from those to which the type species — and eventually other species — of the new genus have been attributed. As a matter of fact, a wrong assignment means obviously that some similarity has been recognized and/or that stress has been untowardly laid on a character without considering its context.

When a new genus is described, its *definition* is made out of a set of internal and external characters, none of which, considered separetely, can be, at the outset, considered as generic. As I have written (1986, p. 142), "It is only after a genus has been sanctioned by usage, i.e. by the adding of species of equivalent age from regions distant from each other, that a generic meaning can be attached to a particular character". In the end it then becomes possible to recognize a genus with the help of the presence or the absence of a restricted number, even one or two, characters. Before this stage is reached it is therefore difficult and dangerous to decree that some differences are "relatively minor" or "inconsequential", while others are important or "real", while still others are omitted, in the circumstances: the thinness of the dental plates, the robustness of the septum, the clearly delimited sulcus and fold starting at a short distance from the beaks, the well-marked costae beginning near the beaks, a.s.o. We are not supposed to choose what fits a purpose, and dismiss the rest; we have to try to read the whole evidence.

When comparing plurispecific genera, it has always been my conservative attitude to restrict the comparison to the *type species* as long as some reservation had to be maintained about the generic ascription of one or more species. This means also that I do not accept the expression "strictly defined genus"; it is a redundancy because a genus is always and permanently defined by its type species as the ICZN reminds us: "the name-bearing type of a nominal genus or subgenus is a nominal species known as the "type species" [Art. 67 (a)].

Finally the *orientation of serial sections* is a false problem that regularly pops up in the literature as often as the Loch Ness monster in the newspapers. One would expect a specialist to be able to recognize and

to interpret the structures revealed by this technique, no matter the orientation of the sections. In order to make comparisons between serial sections made in specimens of various genera easier I have consistently sectioned them along a plane perpendicular to the plane of commissure and to the plane of symmetry. After seventeen years of pondering the problem, I am more than ever convinced that *Ypsilorhynchus* is a valid genus. Not only does the present paper demonstrate that the early Givetian species *Eliorhynchus castanea* cannot be included in it, but also it indicates that I accept in no wise the lowering of *Ypsilorhynchus* to a subgeneric level and its assignment to the genus *Leiorhynchus*. This has commonly been done by North American authors following the lead of JOHNSON (1973, p. 469). Therefore it is clear that I am also opposed to the similar line followed by CHEN (1984, pp. 98-100, 102-103, 122-135, 138, 139), who attributes five, and possibly seven early Frasnian species of southern China to *Ypsilorhynchus,* considered (pp. 99, 102) as included in the genus *Leiorhynchus.* I have already mentioned this opposition (1985, p. 314).

V. - Conclusions

In proposing *Eliorhynchus* n. gen. I am only putting in concrete form what WARREN (1944, p. 112) had already suspected when he questioned the assignment of *E. castanea* to the genus *Leiorhynchus* and suggested that a new genus "may have to be erected". I am also going a step further than JOHNSON (1973, p. 469), who assigned the Canadian species to a subgenus of *Leiorhynchus.* As a result, some early and middle Givetian species are eliminated from the genus *Leiorhynchus.*

References

BASSETT, H.G., 1961. Devonian stratigraphy, central Mackenzie River region, Northwest Territories, Canada. *In*: RAASCH, G.O. (Editor), Geology of the Arctic. Alberta Society of Petroleum Geologists, Proceedings of the First International Symposium on Arctic Geology, University of Toronto Press, 1: 481-498.

BASSETT, H.G. and STOUT, J.G., 1967. Devonian of Western Canada. *In*: OSWALD, D.H. (Editor), International Symposium on the Devonian System, Calgary, 1967. Alberta Society of Petroleum Geologists, 1: 717-752.

BRAUN, W.K., 1966. Stratigraphy and microfauna of Middle and Upper Devonian formations, Norman Wells area, Northwest Territories, Canada. *In*: KULLMANN, J. & WIEDMANN, J. (Herausgeber), Festband Otto H. SCHINDEWOLF zur Vollendung des 70. Lebensjahres am 7. Juni 1966. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* 125: 247-264.

CALDWELL, W.G.E., 1971. The biostratigraphy of some Middle and Upper Devonian rocks in the Northwest Territories: an historical review. *The Musk-ox, Publication* 9: 15-34.

CHATTERTON, B.D.E., 1976. Distribution and paleoecology of Eifelian and early Givetian conodonts from western and northwestern Canada. *In*: BARNES, C.R. (Editor), Conodont Paleoecology, Proceedings of an International Symposium organized by the Geological Association of Canada and the Pander Society and held at the University of Waterloo, Waterloo, Ontario, May 15-17, 1975. *Geological Association of Canada, Special Paper* 15: 143-157.

CHATTERTON, B.D.E., 1978. Aspects of late Early and Middle Devonian conodont biostratigraphy of western and northwestern Canada. *In*: STELCK, C.R. & CHATTERTON, B.D.E. (Editors), Western and Arctic Canadian Biostratigraphy. *Geological Association of Canada, Special Paper* 18: 161-231.

CHEN, Y.-r., 1984. Brachiopods from the Upper Devonian Tuqiaozi Member of the Longmenshan area (Sichuan, China). *Palaeontographica,* A, 184 (5-6): 95-166.

COOPER, G.A. (Chairman), BUTTS, C., CASTER, K.E., CHADWICK, G.H., GOLDRING, W., KINDLE, E.M., KIRK, E., MERRIAM, C.W., SWARTZ, F.M., WARREN, P.S., WARTHIN, A.S. & WILLARD, B., 1942. Correlation of the Devonian sedimentary formation of North America. *Geological Society of America, Bulletin,* 53 (12, pt. 1): 1729-1793.

CRICKMAY, C.H., 1960. The older Devonian faunas of the Northwest Territories. Evelyn de Mille Books, Calgary, 44 pp.

CRICKMAY, C.H., 1963. Significant new Devonian brachiopods from Western Canada. Evelyn de Mille Books, Calgary, 63 pp.

CRICKMAY, C.H., 1967. The method of indivisible aggregates in studies of the Devonian. Evelyn de Mille Books, Calgary, 22 pp.

CRICKMAY, C.H., 1970. Ramparts, Beavertail, and other Devonian formations. *Bulletin Canadian Petroleum Geology,* 18 (1): 67-79.

CUMMING, L.M., 1970. Cf. MCLAREN, D.J.

HOUSE, M.R. & PEDDER, A.E.H., 1963. Devonian goniatites and stratigraphical correlations in Western Canada. *Palaeontology,* 6 (3): 61-114.

JOHNSON, J.G., 1970. Taghanic onlap and the end of North American Devonian provinciality. *Geological Society of America, Bulletin,* 81 (7): 2077-2105.

JOHNSON, J.G., 1973. Late early Devonian rhynchonellid genera from Arctic and Western North America. *Journal of Paleontology,* 47 (3): 465-472.

JOHNSON, J.G., 1974. Middle Devonian Givetian brachiopods from the *Leiorhynchus castanea* Zone of Nevada. *Geologica et Palaeontologica,* 8: 49-95.

JOHNSON, J.G., 1978. Devonian, Givetian age brachiopods and biostratigraphy, central Nevada. *Geologica et Palaeontologica,* 12: 117-149.

JOHNSON, J.G., 1979. Devonian brachiopod biostratigraphy. *In*: HOUSE, M.R., SCRUTTON, C.T. & BASSETT, M.G. (Editors), The Devonian System, a Palaeontological Association International Symposium. *Special Papers in Palaeontology,* 23: 291-306.

McLAREN, D.J., 1962. Middle and Upper Devonian rhynchonelloid brachiopods from Western Canada. *Geological Survey of Canada, Bulletin* 86.

McLAREN, D.J., NORRIS, A.W. & CUMMING, L.M., 1970. Devonian faunas. *In*: DOUGLAS, R.J.W. (Editor), Geology and Economic Minerals of Canada, Chapter XI. Biochronology: Standard of Phanerozoic Time. *Geological Survey of Canada, Economic Geology Report,* 1 (5th edition): 614-622.

MEEK, F.B., 1867. Remarks on the geology of the Valley of Mackenzie River, with figures and descriptions of fossils from that region, in the Museum of the Smithsonian Institution, chiefly collected by the late Robert Kennicott, Esq. *Chicago Academy of Sciences, Transactions,* 1 (1, Art. 3): 61-114.

NORRIS, A.W., 1967. Devonian of northern Yukon Territory and adjacent District of Mackenzie. *In*: OSWALD, D.H. (Editor), International Symposium on the Devonian System, Calgary, 1967. *Alberta Society of Petroleum Geologists,* 1: 753-780.

NORRIS, A.W., 1970. Cf. McLAREN, D.J.

NORRIS, A.W., 1985. Stratigraphy of Devonian outcrop belts in northern Yukon Territory and northwestern District of Mackenzie (Operation Porcupine area). *Geological Survey of Canada, Memoir,* 410.

PEDDER, A.E.H., 1963. Cf. HOUSE, M.R.

PEDDER, A.E.H., 1982. *Chostophyllum,* a new genus of charactophyllid corals from the Middle Devonian of western Canada. *Journal of Paleontology,* 56 (3): 559-582.

SARTENAER, P., 1961. Redescription of *Leiorhynchus quadracostatus* (VANUXEM), type species of *Leiorhynchus* HALL, 1860 (Rhynchonellacea). *Journal of Paleontology,* 35 (6): 963-976.

SARTENAER, P., 1985. The biostratigraphical significance of rhynchonellid genera at the Givetian-Frasnian boundary. *Forschungsinstitut Senckenberg, Courier* 75: 311-317.

SARTENAER, P., 1986. *Hadrotatorhynchus,* genre Rhynchonellide (Brachiopode) nouveau de la fin du Givetien. *Institut royal des Sciences naturelles de Belgique, Bulletin* 56, *Sciences de la Terre*: 137-143.

STELCK, C.R., 1949. Cf. WARREN, P.S.

STELCK, C.R., 1950. Cf. WARREN, P.S.

STELCK, C.R., 1956. Cf. WARREN, P.S.

STELCK, C.R., 1962. Cf. WARREN, P.S.

STOUT, J.G., 1967. Cf. BASSETT, H.G.

UYENO, T.T., 1978. Devonian conodont biostratigraphy of Powell Creek and adjacent areas, western District of Mackenzie. *In*: STELCK, C.R. & CHATTERTON, B.D.E. (Editors), Western and Arctic Canadian Biostratigraphy. *Geological Association of Canada, Special Paper,* 18: 233-257.

WALCOTT, C.D., 1884. Paleontology of the Eureka District. *U.S. Geological Survey, Monographs,* 8.

WARREN, P.S., 1944. Index brachiopods of the Mackenzie River Devonian. *Royal Society of Canada, Transactions, Third Series,* 38 (4): 105-135.

WARREN, P.S., 1957. The Slave Point Formation. *Edmonton Geological Society, Quarterly,* 1 (1): 1, 2, 5.

WARREN, P.S. & STELCK, C.R., 1949. The late Middle Devonian unconformity in northwestern Canada. *Royal Society of Canada, Transactions, Third Series,* 43 (4): 139-148.

WARREN, P.S. & STELCK, C.R., 1950. Succession of Devonian faunas in Western Canada. *Royal Society of Canada, Transactions, Third Series,* 44 (4): 61-78.

WARREN, P.S. & STELCK, C.R., 1956. Reference fossils of Canada. Pt. I, Devonian faunas of Western Canada. *Geological Association of Canada, Special Paper* 1.

WARREN, P.S. & STELCK, C.R., 1962. Western Canadian Givetian. *Alberta Society of Petroleum Geologists, Journal,* 10 (6): 273-291.

WHITEAVES, J.F., 1898. Revision of the nomenclature of some of the species described or enumerated in previous parts of this volume, and additional notes on others, necessitated by the progress of palaeontological research. *Geological Survey of Canada, Contributions Canadian Palaeontology,* I (5), Appendix: 419-427.

SARTENAER, Paul
Département de Paléontologie
Section des Invertébrés primaires
Institut royal des Sciences naturelles
de Belgique
rue Vautier, 29
B-1040 BRUXELLES