Food handling and mastication in the carp (*Cyprinus carpio* L.)

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FOOD HANDLING AND MASTICATION IN THE CARP (*Cyprinus carpio* L.)

Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C.C.Oosterlee,
in het openbaar te verdedigen
op dinsdag 11 december 1984
des namiddags te vier uur in de aula
van de Landbouwhogeschool te Wageningen.

STELLINGEN

1. De taakverdeling tussen de kauwspieren van de karper is analoog aan die tussen vliegspieren van insekten: grote lichaamsspieren leveren indirekt het vermogen, terwijl direkt aangehechte kleinere spieren de beweging vooral sturen. Deze analogie komt voort uit architekturale en kinematische principes.

2. Naamgeving van spieren op grond van hun verwachte rol (b.v. levator, retractor) zonder dat deze feitelijk is onderzocht leidt tot lang doorwerkende misvattingen over hun funktie en geeft blijk van een onderschatting van de plasticiteit waarmee spieren worden ingezet. Een nomenclatuur die gebaseerd is op origo en insertie van de spier verdient de voorkeur.

3. De uitstulpbaarheid van de gesloten bek bij veel cypriniden maakt een getrapte zuivering van het voedsel mogelijk en speelt zo een wezenlijke rol in de selektie van bodemvoedsel. Dit proefschrift.

4. Op grond van de vele funkties die aan slijm in biologische systemen worden toegeschreven is meer onderzoek naar zijn chemische en fysische eigenschappen dringend gewenst. Dit proefschrift.

5. Het samenvallen van het moment van gereedkomen van het kauwapparaat bij de karper (na drie weken; Geyer, 1937) met de overgang naar groter voedsel (Uribe-Zamora, 1975) is begrijpelijk vanuit de eisen die aan de groter wordende vis worden gesteld.

6. De bouw en fysiologie van een soort stellen grenzen aan haar gedrag, en daarmee aan haar positie in een oecosysteem. Deze grenzen vormen belangrijke oecologische parameters maar zijn nauwelijks bekend.

7. Dat het afsterven van bossen pas een prikkel vormt die de aktiedrempel overschrijdt geeft de inflatie in de waardering van milieu-indikatoren schrijnend weer.

8. Optellen, aftrekken, vermenigvuldigen en worteltrekken hebben we goed geleerd. Voor de toekomst moeten we opnieuw leren delen.

9. Onderzoek zou moeten worden gestimuleerd naar optimale organisatievormen om visteelt op ondergelopen landbouwgronden, in waterreservoirs en in irrigatiekanalen een maximale bijdrage te laten leveren aan produkt-diversifikatie en aan de stabilisatie en verdeling van inkomen. Dit zou de plattelandsontwikkeling, met name in ontwikkelingslanden, sterk bevorderen.

10. Het opnieuw inbrengen van de wild-vorm verhoogt de smaak en vitaliteit van de karper (Balon, 1974). Er zijn aanwijzingen dat dit ook voor de kultuur van de mens geldt.

11. De fraaie uitvoering van postzegels uit ontwikkelingslanden is vaak evenredig met de armoede die er heerst en past binnen het verhullende beeld dat het lokale regiem exporteert.

12. Het ontbreken van het jaar van uitgifte op de titelpagina van een wetenschappelijk boek doet vermoeden dat de uitgever nauwelijks prijst stelt op de referentie ervan.

13. De voorgestelde taakverdeling voor UHD's en UD's in het nieuwe rangenstelsel voor wetenschappelijk personeel betekent een achteruitgang voor de benutting, ontplooiing en samenwerking van het personeel.

14. Aanwijzingen dat smaakknopjes van de karper gevoeliger zijn voor menselijk speeksel dan voor een standaardspektrum smaakstoffen (Konishi & Zotterman, 1963) werpt nieuw licht op het met speeksel samenkneden van de deegpluim door hengelaars.

Balon, E.K. (1974). Domestication of the carp *Cyprinus carpio* L.. Roy. Ontario Mus. Life Sci. Misc. Publ.: 1:35.
Geyer, E. (1937). Der Zeitliche Ablauf der Bezahnung und des Zahnwechsels bei *Cyprinus carpio* L., unter besonderer Berücksichtigung des einsömmrigen Karpfens. Morph. Jahrb. 80: 280-354.
Konishi, J. & Zotterman, Y. (1963). Taste functions in fish. In: Olfaction and Taste: 215-233. Y. Zotterman (Ed). New York: McMillan.
Uribe-Zamora, M. (1975). Selection des proies par le filtre branchial de la carpe miroir (*Cyprinus carpio* L.). Thesis, Univ. of Lyon.

Stellingen behorende bij het proefschrift "Food handling and mastication in the carp (*Cyprinus carpio* L.)" door F.A. Sibbing. Wageningen, 11 december 1984.

Voorwoord

Het verschijnen van dit proefschrift biedt mij een welkome gelegenheid allen te danken die aan zijn wording hebben bijgedragen.

Allereerst wil ik mijn ouders bedanken voor de stimulerende vorming en de waardevolle huiselijke sfeer waarin deze plaats vond. Geen inspanning was jullie - ooit te veel. Het baanbrekende werk van mijn oudere broers en zusters waardeer ik zeer.

Jan Osse, de belangstelling voor dit vak moet zeker zijn oorsprong hebben in het niet aflatende enthousiasme waarmee je het vanaf mijn studententijd en ook nu nog steeds uitdraagt. Onze diskussies over de diverse manuskripten hebben in belangrijke mate tot verheldering, relativering en verscherping van hun inhoud bijgedragen. Ik wil je hier graag bedanken voor de stimulerende begeleiding als promotor en voor het initiëren van dit onderzoek.

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Als student hebben Riëtte van Beek, Tonnie te Brinke, Jeannet Ennik, Peter Vossen, Paul van Zwieten en Peter Roessingh steeds een verfrissende en kritische rol vervuld in het onderzoek, dat zich door jullie ook tot andere karperachtige vissen kon uitstrekken. De samenwerking met studenten uit de sectie ethologie (vakgroep Veehouderij), Hans Manni en Arno Brunink, heeft ook mijn kijk op de karper verbreed.

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Cyprinus carpio, dank voor je slijmerige medewerking en de eetlust die je ondanks enige prikakties altijd weer snel aan de dag legde. Onze verschillen in afkomst en milieu hebben een goede samenwerking nooit in de weg gestaan.

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INHOUD / CONTENTS

HOOFDSTUK 1

DOEL VAN HET ONDERZOEK EN SAMENVATTING VAN DE RESULTATEN

Achtergrond van het onderzoek

Vissen vormen een belangrijke schakel op verschillende niveau's in het voedselweb, als prooi maar ook als konsument. De circa 20.000 recente soorten (Nelson, 1976) vormen de grootste groep van de gewervelde dieren en het scala voedseltypen dat zij benutten is groter dan voor elke andere vertebraten groep (Nikolsky, 1963). Maagonderzoek aan vissen, mits uitgevoerd over een groot deel van hun biotoop en zich uitstrekkend over etmaal en seizoenen, geeft een beeld van het dieet van de soort. Het dieet wordt bepaald door de selektieve opname uit een variabel voedselaanbod, vermoedelijk op grond van de smaak en nutriënten van een voedseltype, de tijd die haar verwerking vereist en de verhouding tussen bestede en verworven energie. Verschillen in plaats, grootte, vorm, beweeglijkheid, chemische en mechanische samenstelling van het voedselaanbod doen ons specialisaties verwachten in bouw, funktioneren en gedrag van de vis. Deze blijken mede uit het naast elkaar aanwezig zijn van vele vissoorten in één levensgemeenschap. Welke deze specialisaties zijn, hoe zij het dieet begrenzen en hoe zij de konkurrentiepositie van de vis bepalen is nauwelijks bekend. De gevolgen van opzettelijke of toevallige ecologische veranderingen in het milieu op de trofische relaties en samenstelling van de visfauna zijn dan ook niet voorspelbaar. Dit blijkt ondermeer bij introduktie van uitheemse vissoorten. Inzicht in de relaties tussen de vis en zijn omgeving vereist een gekombineerde aanpak van funktionele morfologie, ethologie en ecologie. Kennis hiervan kan richting geven aan de beheersing van natuurlijke en kunstmatige aquatische systemen.

Door de bovengenoemde specialisaties te onderzoeken wordt inzicht verkregen in de grondslagen van bouw en werking van het sensorisch, het motorisch en het regelapparaat voor de voedselopname. Deze dragen tesamen zorg voor zoeken, detektie, opname en verwerking van het voedsel.

Karperachtige vissen

De karper (*Cyprinus carpio* L.) werd als onderzoeksobject gekozen op grond van de volgende argumenten.

1) Karperachtigen (*Cyprinidae*) vormen met 1600 soorten de grootste familie van vissen (Nelson, 1976). Over hun voedselverwerkingsmechanisme is vrijwel niets bekend.

2) In Nederland is deze familie in het zoete water het sterkst vertegenwoordigd in aantal soorten (20) en biomassa.
3) Zij tonen een grote variatie in ecologische en trofische typen. Zo worden voor een maximale benutting van het voedselaanbod in vijverkulturen zoöplanktivoren, fytoplanktivoren, macrofytofagen, omnivoren en bodemvreters gemengd geteeld (Bardach et al., 1972). De graskarper wordt ingezet bij de biologische kontrole van plantengroei in watersystemen.
4) De karper wordt op grote schaal gekweekt en vormt enerzijds een gewaardeerd voedsel (Oost-Europa, Azië), maar kan door explosieve aantalsvermeerdering ook tot plagen leiden (N-Amerika, Australië).
5) De karper is als proefdier de 'laboratorium-rat' onder de vissen. Een synthese van gegevens met die uit andere vakgebieden verdiept onze kennis over deze zeer algemeen voorkomende vis. Gegevens over darminhoud zijn in de literatuur op ruime schaal voorhanden.

Cypriniden vormen ook uit morfologisch oogpunt een bijzondere familie. Tanden op de kaken en in de mondholte ontbreken; de laatste kieuwbogen zijn tot sterk ontwikkelde tandendragende keelkaken omgevormd die samen met een hoornplaat in de schedelbasis een krachtig kauwsysteem vormen (Fig. 1, pag. 129). De maag ontbreekt bij alle soorten. De sterke ontwikkeling van het kauwapparaat in de keel ontlast de mondkaken van een bijtfunktie en heeft mogelijk zo bijgedragen tot de ontwikkeling van een uitstulpbaar mondapparaat, dat uniek is onder de lagere beenvissen (slot hoofdstuk 2).
Samen met de vier andere suborden van de Ostariophysi (Chanoidei, Gonorynchoidei, Characoidei, Siluroidei; Roberts, 1973; Fink and Fink, 1981) bezitten de Cyprinoidei alarmcellen (p. 110) en het apparaat van Weber, een verbinding tussen zwemblaas en gehoorstreek die voor geluidswaarneming dient (Alexander, 1967).

Probleemstelling en methoden

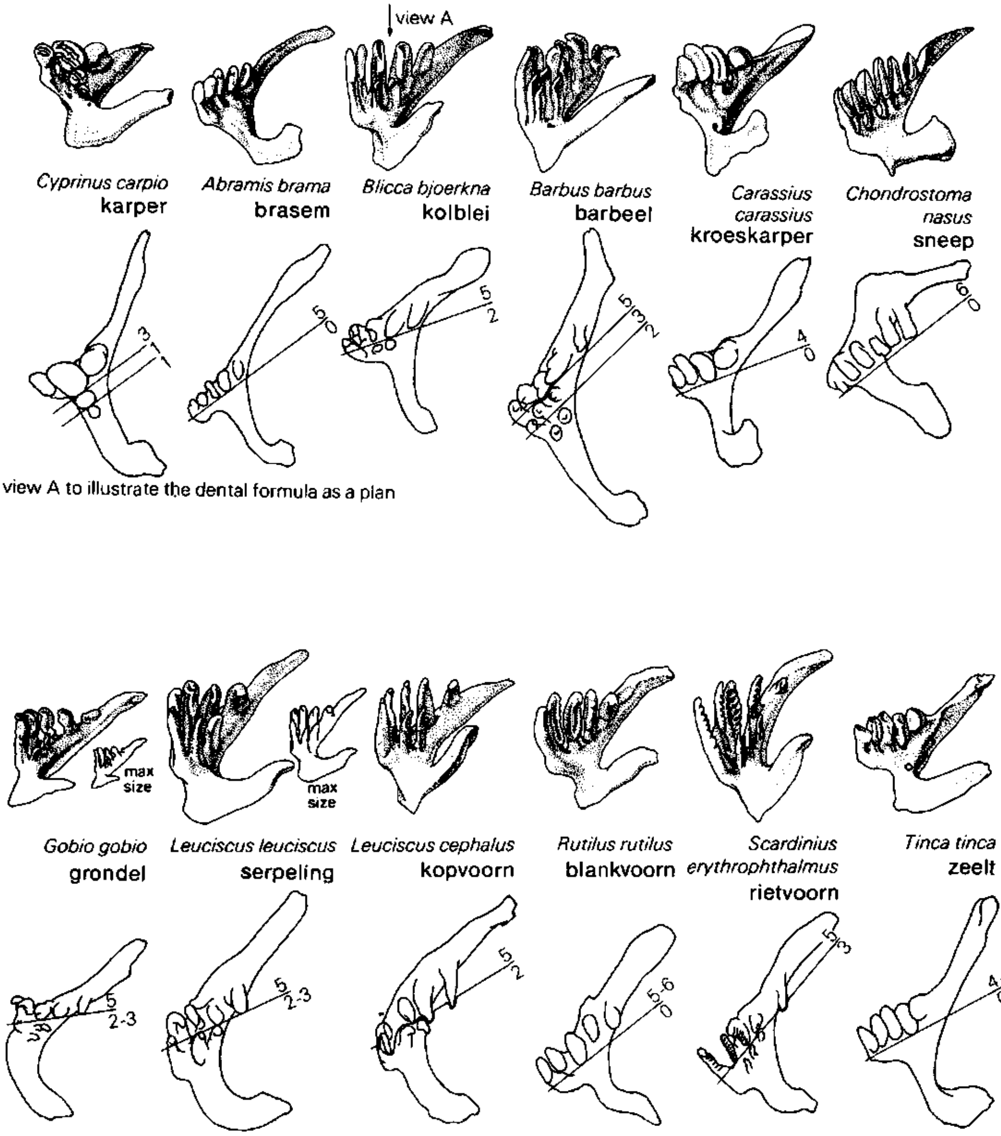
De *funktionele morfologie* onderzoekt de samenhang tussen bouw en funktie in een biologisch systeem, er van uitgaand dat hierop, op grond van fysische wetten, in de natuur wordt geselekteerd. De vorm-funktie relatie kan door vergelijking van bestaande strukturen en hun funkties worden bepaald (induktie). Zij kan ook door deduktie van een theoretisch fysisch model, dat aan bestaande vormen wordt getoetst, vanuit de funktie worden vastgesteld (Dullemeijer, 1974). Vaak worden beide en de experimentele methode (bijv. aanbod van verschillende voedseltypen) in kombinatie toegepast.

Ofschoon de vis als samenhangend geheel funktioneert, wordt hij bij vormanalyse opgedeeld in strukturen van verschillend weefseltype (bv. beenelementen, spieren, ligamenten). Struktuurkomplexen die een specifieke funktie uitoefenen noemen we funktionele komponenten (van der Klaauw, 1945; Dullemeijer, 1974). Deze kunnen zich tot het hele organisme uitstrekken (bv. voortbewegingsapparaat) maar men kan dit begrip ook toepassen op niveau van een spiervezel (cf. Akster, 1981). Inzicht in de vorm-funktie relaties binnen een funktionele komponent is pas goed mogelijk wanneer ook de wederzijdse afhankelijkheid van zulke komponenten in het onderzoek worden betrokken. Zo maken strukturen van het voedselopname apparaat van de karper (bv. de sternohyoideus spier) tevens deel uit van het ademhalingssysteem en het kauwapparaat (p.149). Bij deze integratie stellen verschillende funkties eisen aan eenzelfde struktuur. Integratie van struktuurkomplexen voor deelfunkties in het geheel van de vis betekent dan ook vaak een inperking van de vrijheid om deelfunkties optimaal te realiseren (cf. Barel, 1983). Een holistische benadering vormt daarom het uitgangspunt voor de analyse van het voedingssysteem en zijn deelfunkties.

Opvatting van het begrip 'funktie' als de 'biologische betekenis van een aktie in de natuurlijke omgeving' is impliciet aan het onderzoeksthema van de sektie funktionele diermorfologie van de Landbouwhogeschool: *'Voedselopname en -verwerking bij vissen: eco-morfologische aspekten'*. Dit betekent voor de toekomst van het onderzoek dat de wijze waarop de vis het voedselaanbod in zijn natuurlijke omgeving benut een noodzakelijk onderdeel van de studie moet zijn, meer dan tot nu toe gerealiseerd kon worden.

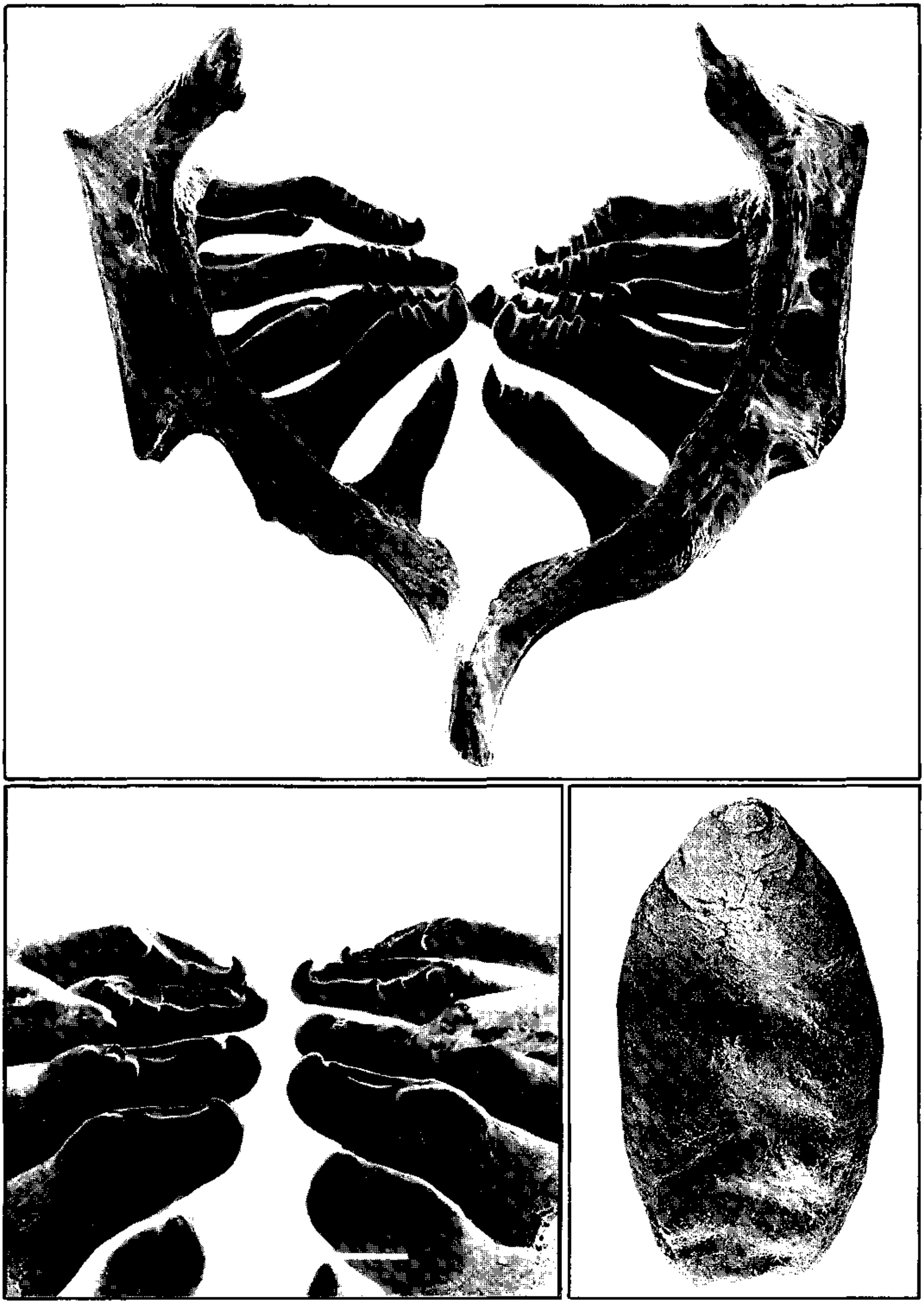
Vergelijking van de vormenrijkdom in het voedselopname-apparaat der cypriniden en hun leefwijze leidde tot gewaagde uitspraken over specialisaties waarbij de funktie vooral uit de bouw werd afgeleid (Suyehiro, 1942; Al-Hussaini, 1949; Matthes, 1963; Verighina, 1969; Kapoor et al., 1975).

Een gedetailleerd onderzoek van bouw èn functie van het voedselopname-apparaat werd gestart bij vissen van het baars-type (*Percoidei*) (Osse, 1969; Liem, 1973). Het zuigproces bij de voedselopname van cypriniden werd voor het eerst via meting van waterdruk in de mondholte door Alexander (1969) bestudeerd. Het gekompliceerde proces van voedselverwerking ná opname vindt binnen de mond- en keelholte plaats. Een analyse van de reeks van deelprocessen, die hierbij optreedt werd niet eerder uitgevoerd. De opvallend gevarieerde keelkaken en -tanden (Fig. 1) worden bijvoorbeeld als determinatie sleutel gebruikt en hun overeenkomst in bouw als argument voor verwantschap gehanteerd (Hensel, 1970). De samenhang tussen bouw en funktie van het kauwapparaat en de wisselwerking tussen deze en andere funktionele komponenten in de kop is niet onderzocht. Met andere woorden, keelkaken



naar Wheeler (1978)

FIG. 1. Rechter-keelkaken met keeltanden van enkele der 20 karperachtige vissoorten, die in de Nederlandse binnenwateren voorkomen. Let op de verschillen in tandbouw en tandformule. De keelkaken werken als paar tegen een verhoornde kauwplaat (vgl. Plaat I) in het gehemelte van de vis. Zij zijn in grootte, stevigheid en ruimtelijke bouw (uitstekende armen) sterk gevarieerd.



PLAAT I. SEM-beeld van de keelkaken van de rietvoorn (16.1 cm; boven) en van de keeltanden en verhoornde kauwplaat van de blankvoorn (21 cm; onder). De detaillering in de tandsculptuur verschilt vooral vooraan sterk en houdt verband met het uiteenlopende dieet van deze uitwendig op elkaar gelijkende vissen. Terwijl beiden ondermeer insektelarven en plantedelen eten, heeft de blankvoorn ook vooral slakken op het menu.

van cypriniden worden algemeen als kenmerk gebruikt maar hun invloed op het bouwplan van de hele vis en hun specifieke rol in de kompetitie tussen soorten is onbekend.

De vraagstelling die aan dit proefschrift ten gronde ligt is vierledig:

1) *Uit welke delen bestaat het proces van de voedselopname en -verwerking bij de karper?*
2) *Welke strukturen zijn bij elk deelproces betrokken en hoe is de samenhang tussen hun bouw en funktie?*
3) *Hoe beïnvloeden de deelprocessen elkaar en vindt afstemming van het totaalproces plaats in relatie tot de aard van het voedsel?*
4) *Welke beperkingen in het gebruik van het voedselaanbod zijn het gevolg van de 'omnivorie' van de karper en de daarbij horende aanpassingen in bouw en funktie?*

De vraagstelling richt zich op het niveau van het totale funktionerende dier. Het onderzoek is er op gericht om de funktie uitoefening aan de zoveel mogelijk ongestoorde vis te meten.

Gedetailleerde gegevens omtrent bouw en funktioneren werden verkregen met de volgende technieken:

- macroscopische, microscopische en scanning-electronen-microscopische (SEM) vormanalyse. Uit coupe-series werd het verspreidingspatroon van smaakknopjes, slijm, spierweefsel en alarmcellen in de mond-keelholte gemeten. Het slijm werd histochemisch onderzocht.
- afleiding van spieractiviteiten via electromyografie (9 kanalen), al dan niet in kombinatie met gewone of röntgen-film.
- meting van uitwendige en inwendige bewegingen van kopdelen bij aanbod van verschillende voedseltypen: pellets, gerstkorrels, regenwormen, tubifex, watervlooien en bodem-tubifex mengsels. Door het aanbrengen van bariumsulfaat in pellets en wormen kan de procesgang van dit voedsel in de röntgenfilm worden gevolgd.

Analyse heeft dus ook plaatsgevonden op het niveau van weefsel en cel alsmede op het niveau van de motorische aktiviteit binnen afzonderlijke spieren. Anderzijds vereist inzicht in de relatie tussen bouw van het organisme en zijn funktioneren in een natuurlijke omgeving, zoals eerder aangegeven, diepgaande analyse van het natuurlijk gedrag en zijn ecologische niche. Niet elk van deze aspekten kon op gewenste diepte worden onderzocht, vaak werd hiervoor naar literatuurgegevens teruggegrepen.

De gegevens worden benut om ook de vraag naar de evolutie van de strukturele kenmerken te behandelen.

De verkregen kennis geeft een samenhangend beeld van de zich voedende karper en levert een nieuw vertrekpunt op voor gespecialiseerd onderzoek naar aanpassingen in bv. zintuigen en slijm, naar de neurale regulatie van de voedselverwerking en naar de efficiency waarmee verschillende voedselbronnen in een natuurlijke situatie worden benut.

De resultaten van het onderzoek zijn verwerkt in de hoofdstukken 2, 3 en 4, waarvan de inhoud hieronder kort wordt genoemd.

In Hoofdstuk 2 wordt de totale procesgang en de afzonderlijke mechanismen voor de opeenvolgende fasen van voedselverwerking tesamen met zijn plasticiteit en beperkingen besproken.

Hoofdstuk 3 geeft een macro- en microscopische analyse van de mond-keelholte bekleding en relateert deze aan deelfunkties van het voedingssysteem.

In Hoofdstuk 4 worden vorm-funktie relaties binnen het kauwsysteem van de karper in detail uitgewerkt. Hierin is ook een globaal beeld van het dieet van de karper opgenomen (pag. 138).

Voedselopname en voedselverwerking door de karper

Het voedselopname en -verwerkingsproces valt uiteen in een aantal herkenbare deelprocessen (Fig. 2) die, aangepast aan het type voedsel, in herkenbare volgorde worden ingezet: zoeken, detektie, opname, selektie door proeven en reiniging, transport, kauwen en slikken (hoofdstuk 2). Vertering valt buiten het bestek van deze studie maar werd eerder voor cypriniden overzien en bij de graskarper bestudeerd door Stroband (1980).

Wat eet de karper?

Resultaten voortkomend uit darminhoud onderzoek worden met hoge frekwentie gerapporteerd. Uribe-Zamora (1975) stelde hierin de grote lijn vast (p.138). De volwassen karper blijkt een omnivore vis, die zich, afhankelijk van het watersysteem en seizoen, vooral met de volgende organismen voedt: 1) bodem-evertebraten (muggelarven, tubifex, copepoden, mollusken, andere insektenlarven), 2) zoöplankton (de grotere soorten watervlooien en copepoden), 3) littorale vegetatie (vooral zachtere waterplanten als eendenkroos) en dieren die zich daartussen bevinden (slakken, copepoden, kokerjuffers en wormen).

Hoe en wanneer zoekt de karper zijn voedsel?

Jönsson (1967) heeft in laboratorium-studies het voedselopname gedrag van éénzomerige karpers uitvoerig onderzocht. Het door interne faktoren bepaalde deel van de zoekaktiviteit heeft een hoge piek in de schemering en 's nachts. Konditionering op uitwendige faktoren als voedertijd en -plaats vindt, ook overdag, gemakkelijk plaats. Detectie van voedsel gebeurt vooral met behulp van smaakzintuigen op baarddraden en lippen, die hij in kontakt met de bodem brengt. Geleiding naar voedsel over langere afstand vindt waarschijnlijk via de reuk plaats. Het oog speelt vooral bij bewegende prooi een rol, voor zover de troebeling van het water dit toelaat. De ondergrens van de lichtintensiteit voor effektieve lokalisatie van voedsel ligt voor de meeste vissen bij 10^{-1}mc (meter-candela), overeenkomend met late schemering (Blaxter, 1970). Hele graankorrels, vaak gevoerd in de karperteelt, werken niet of nauwelijks stimulerend. Konditionering of bijmenging van stimulerend voedsel verhoogt de opname. Zelfs van de karper blijken weinig gegevens bekend over zijn voedselopnamegedrag in het natuurlijk milieu. Dit hangt samen met problemen van waarneming.

Baarddraden en lippen zijn bezet met hoge dichtheden smaakknopjes (ca. 380 per mm^2; Plaat I, pag. 88). De hoge lichaamsbouw - die in snelstromend water tot afdrijven zou afleiden - en de overheersing van rode, langzaam kontraherende maar niet snel vermoeibare spiervezels in de romp passen bij het langzaam zwemmend zoeken, dat zich over lange periodes uitstrekt (stayer; Boddeke, Slijper en van der Stelt, 1959). Snelle prooien hebben hierdoor een relatief grote ontsnappingskans.

Hoe vindt voedselopname plaats?

Afhankelijk van het type voedsel treden verschillende mechanismen voor opname in werking. Afbijten van voedselbrokken is met de tandeloze kaken vrijwel onmogelijk, de verhoornde kaakranden (Plaat III a, pag. 92) spelen een rol bij het manipuleren van groter materiaal (macrofyten, steentjes).

Opname van deeltjes (Particulate feeding, Fig. 5, pag. 60). Moeilijk bereikbaar en zwaar voedsel, door de maten van de mondopening beperkt tot deeltjes met een diameter kleiner dan ca. 9% van de standaardlengte van de vis, wordt opgenomen door aanzienlijke expansie van de mond- en kieuwholte (terminologie in Fig. 1, pag. 37) onder gelijktijdige protrusie (uitstulping) van de bovenkaak. Dit bewegingspatroon wekt een grote snelheid van het water op in de mondopening (ca. 60 cm/sec.), sterk gericht op het voedsel. Modifikatie van de protrusierichting laat bijregeling van de zuigrichting t.o.v. het voedsel toe. Protrusie kan de mondopening van een vrijwel eindstandige in een onderstandige positie brengen, hetgeen de vis in staat stelt de bodem al zwemmend af te zoeken, zonder dat een voortdurende standsverandering van het lichaam nodig is.

Slokken (Gulping, Fig. 6, pag. 60). Gesuspendeerd materiaal wordt met kleine slokjes over langere periodes herhaald opgenomen (vgl. Janssen, 1976). De expansie van de kieuwholte speelt nu voor de opname zelf een ondergeschikte rol, de suspensie wordt vooral door depressie van de mondholte langzaam opgenomen en kan ook via de mondhoeken binnentreden. De karper stulpt zijn bovenkaken pas laat en naar beneden uit, vormt daarmee een kap over de suspensie en sluit zo zijn bek. Uitstoting van deeltjes bij de nu volgende kompressie van de mondholte wordt zo voorkomen. Gulping wordt vooral bij het grazen van plankton toegepast maar ook bij bodemvreten wanneer materiaal door spuwen in suspensie raakt. Grote volumina water worden over lange periodes verwerkt zonder dat het water sterk versneld wordt. De afzonderlijke slok kost hoogstwaarschijnlijk minder energie dan gerichte opname van partikels, omdat de expansie in omvang en snelheid beperkt is en de kieuwdekselklep vroeg opengaat.

Op grond van observaties van het opnamegedrag van zoöplankton, de detectiemogelijkheden van de zintuigen, en berekeningen die aangeven dat de vis gedurende 24 uur 1.000.000 maal zijn bek zou moeten openen en sluiten om in zijn voedselbehoefte te voorzien, wordt het sterk betwijfeld of de karper bij opname van zoöplankton gericht partikels uitkiest (Jönsson, 1967). Opname via slokjes met een grote partikeldichtheid lijkt, gezien de voor opname benodigde tijd en energie, voor de karper het meest efficiënt. Ook bij andere vissen is het gedrag bij selektieve opname van zoöplankton in relatie tot de energie opbrengst een belangrijk onderzoeksthema (cf. Wright and O'Brien, 1984).

Retentie van partikels in de keel

Grote partikels worden bij opname gevangen in de nauwe doch brede keelspleet, die in tegenstelling tot de situatie bij veel niet-cypriniden, slechts beperkte volumeveranderingen ondergaat. Fijn verdeeld voedsel dringt verder in de keelspleet door en verzamelt zich op de kieuwzeef (Plaat I, pag. 88), die partikels kleiner dan 250 µm (karpers 150-1500 gram; Uribe-Zamora, 1975) met het water naar buiten laat.

De werking en efficiency van de kieuwzeef valt buiten het bestek van dit proefschrift en wordt bij de brasem onderzocht door A.G.Kroon via een BION/ZWO-project in samenwerking met het Limnologisch Instituut van de KNAW.

Hoe vindt scheiding van eetbare en niet-eetbare deeltjes plaats?

Bij het bodemvreten van de karper vindt waarschijnlijk wel een grove keuze van het substraat plaats, doch de feitelijke selektie tussen voedsel en onbruikbaar

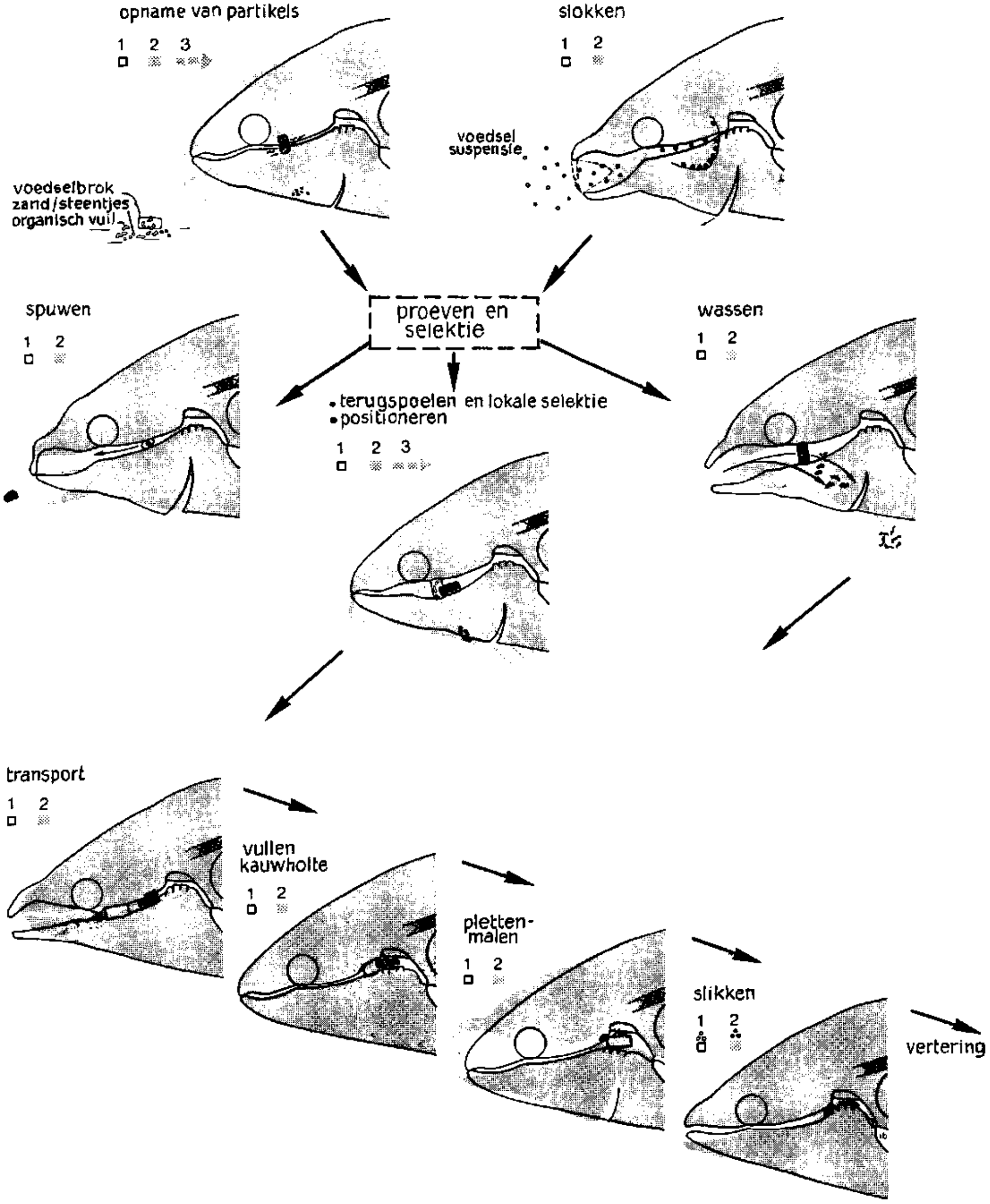


FIG. 2. Bewegingspatronen van de karper behorende bij de mechanismen voor opname en verwerking van verschillende typen voedsel (b.v. bodemmateriaal, zoöplankton). Afhankelijk van plaats, grootte, smaak, verontreiniging en mechanische eigenschappen van het voedsel worden de patronen met wisselende frekwenties in het totaalproces geïntegreerd (vgl. resp. deeltjes opname – slokken, spuwen – terugspoelen en lokale selektie – wassen, pletten – malen). De volgorde der fasen is bij elk patroon aangegeven. Verdere toelichting bij de figuren in hoofdstuk 2.

materiaal treedt ná opname in de mondkeelholte op. Welke aspekten in bouw en aktie stellen de karper tot een zo gespecialiseerde voedselexploitatie in staat?

Het palataal orgaan van de karper, een omvangrijk en complex gebouwd spierkussen in het gehemelte, is bezet met welhaast maximale dichtheden smaakknopjes ($820/mm^2$; hoofdstuk 3). Dit stijgt ver uit boven waarden bij andere vissen, voorzover gemeten. Reeds in 1827 werd dit orgaan door Weber een rol bij selektie toegeschreven. Regionale analyse van bouw en aktiviteit van het palataal orgaan en zijn analogon in het midden van de keelbodem, het postlinguale orgaan (Plaat II d, pag.90), toont hun funkties in de voedselverwerking. Drie niveau's van beweging worden voorgesteld (pag. 113): 1) beweging van het palataal orgaan als geheel als gevolg van aktiviteit in de dorsale kieuwboogspieren, 2) regionale zwellingen en peristaltiek en 3) zeer lokale beweging van gespierde papillen in het palatale oppervlak. Dit leidt tot het volgende beeld voor het selektiemechanisme tussen voedsel en niet-voedsel.

Zware anorganische partikels als zand en grind zinken wellicht voor het grootste deel direkt door de wijde eerste kieuwspleet, lichte organische verontreinigingen komen met het voedsel in de keel. De grote dichtheid aan smaakknopjes en spiervezels, vooral in het palataal orgaan maar ook op de kieuwzeef, vormen de basis voor een mechanisme waarbij voedsel waarschijnlijk door lokale bultvorming tussen keeldak en keelbodem kan worden vastgezet. Niet-eetbare partikels worden niet vastgezet en bij kompressie via de kieuwspleten met het water naar buiten gespoeld. De nauwe keelspleet levert een groot selektie oppervlak. De grote dichtheid aan smaakknopjes, het papillen- profiel van zowel spierkussenoppervlak als kieuwzeef, en de gemeten differentiatie in lokale aktiviteit van het palataal orgaan duiden op een groot scheidend vermogen. De laminaire cyto-architektuur van de vagus lob in de nauw verwante goudvis suggereert bovendien palatotopie. Deze ruimtelijke afbeelding van de informatie uit het palatale orgaan in de hersenen is vermoedelijk een voorwaarde voor een zeer lokale bewegingssturing (cf. Finger, 1981). Dat dit mechanisme niet direkt een volledige scheiding teweeg brengt blijkt uit de herhaalde terugspoelbewegingen naar de mondholte (back-washing), waarin resuspensie van het materiaal voor een volgende selektiefase plaatsvindt, en uit de geringe verontreinigingen in de darm. Protrusiebewegingen met gesloten bek veroorzaken het terugspoelen naar de mondholte en zijn bij dit getrapte zuiveringsproces van essentieel belang. Zij maken de mondholte tot een spoelkamer (Fig. 8, pag.64).

Grove zuivering van grote voedselbrokken, die het kontakt tussen keelbodem en keeldak beperken, kan ook door intensief wassen via pompbewegingen met een van mond- naar kieuwholte gerichte waterstroom plaatsvinden (rinsing). Bij sterk verontreinigd of moeilijk hanteerbaar voedsel treedt meestal resuspensie door spuwen en her-opname op.

Uitspuwen van onsmakelijk of zelfs toxisch voedsel (bv. watermijten) is een bekend fenomeen, ook bij vissen. Partikels worden bij gesloten bek door expansie van de mondholte naar voren gespoeld en daarna door adductie van de kieuwdeksels via de mond uitgestoten (Fig. 9, pag.66).

Slijmkleuringen in de mond-keelholte tonen de aanwezigheid van minstens twee verschillende typen slijm aan (hoofdstuk 3): sialomucines met relatief lage viskositeit in de mond en voorste keelholte, sulfomucines met relatief hoge viskositeit (Hunt, 1970) achter in de keelholte. Het weinig viskeuze slijm langs de weg van het water dient behalve als bescherming waarschijnlijk ook om turbulenties in de grenslaag langs de wand te verminderen en daarmee de weerstand voor watertransport te verkleinen (Rosen & Cornford, 1971). Sterk viskeus slijm achterin de keel bevordert waarschijnlijk het vangen van kleine partikels en hun samenklontering. De afwezigheid van dit slijmtype in het voorste deel van de mond-keelholte laat effektieve resuspensie van het materiaal bij zuivering toe. Deze en andere funkties van slijm (bv. smering bij transport) komen ter diskussie in hoofdstuk 3.

Hoe wordt geselekteerd voedsel naar de kauwholte getransporteerd?

Voor zover het voedsel nog niet achter in de keelholte tussen palataal en postlinguaal orgaan ligt wordt het door gesloten protrusiebewegingen teruggespoeld en door gekoördineerde aktie van het palataal orgaan en de keelbodem in deze transportpositie gemanoeuvreerd (repositioning). Voedselpartikels uit de kieuwzeef worden welhaast zeker op eenzelfde wijze door terugspoeling verzameld.

Tandendragende kieuwboogelementen in het keeldak zorgen voor transport bij de meeste niet-cypriniden (Liem, 1973; Lauder, 1983), maar ontbreken bij karperachtige vissen. Gekoördineerde kontrakties in het achterste deel van palatale en postlinguale orgaan drijven het voedsel langzaam (2-3 cm/sec.) met peristaltische golven tot in de kauwholte voort (Fig. 10, pag. 67). De rol van de sterk toegenomen slijmproduktie in dit gebied (sulfomucines) werd reeds vermeld. De dichtheid aan smaakknopjes neemt in deze zelfde richting af (Fig. 7 , pag. 107).

Hoe vindt de mechanische verkleining van het voedsel plaats?

Het kauwsysteem dient er toe het voedsel zodanig te vervormen, dat het oppervlak voor de inwerking van spijsverteringsenzymen wordt vergroot en om slecht doordringbare kapsels te breken. Gezien het ontbreken van een maag is dit van groot belang bij karperachtigen.

In tegenstelling tot zoogdierkaken hebben de keelkaken van de karper een groot aantal vrijheidsgraden (4) in beweging. Ze zijn onderling beweeglijk en via negen paar spieren aan schedel, schoudergordel en kieuwkorf opgehangen. Een glijkoppeling tussen keelkaken en kieuwbogen laat rostro-caudale translatie toe. De beweging van deze kaken tegen de kauwplaat van de schedel is verder samengesteld uit rotaties om vier verschillende anatomische assen (hoofdstuk 4). Het kauwproces verloopt bilateraal synchroon en is opgebouwd uit een of meer kauwtreinen, elk samengesteld uit series kauwslagen. Op grond van bewegings- en aktiviteitspatroon van de kauwspieren worden plet- en maalslagen (resp. crushing en grinding) van elkaar onderscheiden.

De belasting van het voedsel (kompressie, rek, afschuiving, torsie en buiging) hangt af van de profielen van de occlusievlakken (tanden en maalplaat) en de richting waarin zij ten opzichte van elkaar bewegen. Het heterodonte kauwapparaat van de karper (Fig. 2, pag.129) is slecht uitgerust voor snijden, knippen en uiteentrekken van voedsel maar biedt goede mogelijkheden tot pletten en malen (p.153). Het kauweffekt hangt af van de mechanische eigenschappen van het aangeboden voedsel. Brosse en stijve materialen worden verbrijzeld, meer elastisch, taai en/of vezelig voedsel wordt vooral geplet. De kauwholte kan slechts beperkt expanderen, delen met een diameter groter dan ca. 3% van de lichaamslengte kunnen er niet in. Het grote kauwoppervlak, de lengte van de kauwslag en ook de aanwezigheid van zandkorrels in de tandgroeven bevorderen de vermaling van kleine partikels, kwantitatief en kwalitatief.

Welke kauwdruk kan dit systeem produceren? Dit hangt in de eerste plaats af van het kontaktoppervlak tussen occlusievlakken en voedsel en zal dus met de vorm en grootte van het voedsel variëren. Ofschoon de positie van de kauwholte, midden in de kop, kauwdrukmetingen in de weg staat, geeft vorm-funktie onderzoek aan dat de kauwkracht groot is. Als argumenten hiervoor gelden ondermeer:

1) De direkt op de keelkaken aangehechte spieren stralen wijd uit naar omringende beenelementen, maar hun werklijnen vormen gunstige rotatie-koppels rond de onderhavige assen. Hierdoor worden de krachten van de afzonderlijke spieren sterk gebundeld (vgl. Fig. 7 pag.134).
2) De keelkaken vormen lange uitsteeksels en vleugels die, behalve dat zij spieren een groot oppervlak voor aanhechting bieden, grote momentarmen leveren. De kauwvlakken liggen dicht bij de rotatie-assen van de keelkaken en brengen zo vergrote krachten op het voedsel over. Alleen de transversale as, voorin door de symfysis van de keelkaken, ligt ver van de tanden verwijderd en laat grotere amplitudes van de keelkaken toe. Dit is van belang tijdens expansie van de kauwholte bij het opladen van het voedsel.
3) De rug- en buikspieren van de karper zijn tijdens het kauwen actief en dragen

hun krachten op de kauwplaat en keelkaken over via resp. de schedel en de schoudergordel en via kauwspieren met pezige komponenten. Vergeleken bij de direkte kauwspieren leveren zij een zeer groot vermogen (vgl. Fig. 20, pag.155).

4) De hoge schedel en lange schoudergordel vormen grote momentarmen voor deze lichaamsspieren. De ligging van de kauwplaat vlak onder het rotatiecentrum van de schedel resulteert in een kleine doch zéér krachtige beweging van de kauwplaat, tegengesteld aan die van de tanden. De kauwplaat werd in de literatuur tot nu toe door haar fixatie in de schedelbasis zonder uitzondering van de kauwbeweging uitgesloten.

De grote kauwkracht stelt eisen aan het kauwapparaat wat betreft sturing, stabilisatie en absorbtie van reaktiekrachten. Dit is des te meer van belang daar de keelkaken in spieren zijn opgehangen en het hart van de vis direkt tussen de keelkaken ligt en door deze overdekt wordt (Plaat II d, pag.90). Sturing en stabilisatie wordt behalve door ligamenten tussen en achter de keelkaken vooral ook bereikt door de geprogrammeerde aktie van de kauwspieren, die elkaar door antagonistische werking in effekt balanceren (Fig. 15, p.147). De pharyngo-cleithralis externus spier speelt hierbij een sleutelrol. Beenbalkjes die zowel vanuit de tanden over de keelkaken als vanuit de kauwplaat-kom over de schedelbasis uitstralen zorgen voor een gelijkmatige spreiding van reaktiekrachten en voorkomen zo te sterke belasting van het eigen systeem.

De vereiste rotatieslag van de keelkaken is ondermeer mogelijk dankzij de glijkoppeling in de basis van de kieuwkorf. De aktiviteit van de spierketen in de bodem van de kop draagt zowel bij in voor- en achterwaartse bewegingen van de schoudergordel bij het kauwen, als tot het vergroten van de slagruimte van de keelkaken. De sterke expansie van de kop en het open gaan van de bek bij het kauwen is meer een gevolg van het kauwproces dan dat het tot voedselopname of respiratie dient. Het kauw- en ademhalingsritme verschillen overigens niet belangrijk.

Het kauwapparaat beperkt zich dus niet tot de keelkaken en de daarop aangehechte spieren. Kauwen vereist bewegingen van de kop als geheel en van de rug en buik van de vis en beperkt daarmee het gelijktijdig uitvoeren van andere funkties (bv. respiratie, opname, selektie). De rotatie van de schedel tot ca. 15° maakt tevens de loop van de botjes van Weber, dicht langs het rotatiecentrum van de schedel welhaast tot een strukturele noodzaak. De opbouw van deze verbinding tussen middenoor en zwemblaas uit vele elementen lijkt een kompromis, dat zowel het overbrengen van trillingen als de beweging van de schedel bij het kauwen toelaat. Het is te verwachten dat de frekwentie gevoeligheid van het gehoor en de bij het kauwen geproduceerde trillingen weinig overlap hebben. Bij het breken van maiskorrels zijn de kauwslagen van de karper tot buiten het aquarium hoorbaar!

Het doorslikken van het voedsel

Transport van verkleind voedsel naar de darm geschiedt door middel van kompressie van de kauwholte door de constrictor pharyngis spier, ondersteund door een kleine beweging van de keelkaken. Het palataal en postlinguaal orgaan sluiten door opzwelling de toegang tot de kauwholte af en richten daarmee het transport naar de slokdarm. Aktiviteit van de constrictor pharyngis zet zich wellicht peristaltisch in de slokdarm voort.

Hoe stemt de karper zijn gedrag af op de eigenschappen van het voedsel?

De procesgang bij verwerking van verschillende typen voedsel (pellets, gerst, worm, tubifex, watervlooien, bodem-tubifex mengsels) duidt er op dat bovengenoemde deelprocessen een in beweging en aktiviteit stereotyp karakter dragen ('fixed action patterns'?; Baerends, 1979). Zij kunnen als herkenbare eenheden van gedrag worden onderscheiden. Afhankelijk van positie, grootte en aard van het voedsel worden zij in herkenbare volgorde maar met wisselende frekwentie ingezet (bv. partikel opname-slokken, pletten-malen), hetgeen leidt tot variaties in het totale verwerkingsproces (hoofdstuk 2, pag. 56). De voor de totale voedselverwerking bij één opname benodigde tijd (handling time) kan direkt uit de electromyogrammen worden afgelezen en blijkt voor verschillende voedseltypen sterk te verschillen (Fig. 3-4, p. 53). Zij wordt vooral bepaald door herhaling van voor een voedseltype specifiek benodigde deelprocessen. Zo is de 'handling time' voor grote partikels vooral door herhaald kauwen lang, terwijl bij verontreinigd voedsel voortdurend terugspoelen bij selektie veel tijd vergt. Gesloten protrusie blijkt een kernpatroon, dat aan de basis ligt van meerdere deelprocessen (positioneren, terugspoelen, verzameling voedsel van de kieuwzeef), die op grond van hun effekt op het voedsel worden onderscheiden. Spuwen en monsteren van bodemmateriaal (probing) leiden niet tot opname in het darmkanaal en worden als aparte sequenties onderscheiden.

De mechanismen die deze gedragskomponenten opwekken, vasthouden en stoppen zijn onbekend, evenals de regulatiemechanismen die de deelpatronen tot een efficiënt voedingsproces samenvoegt. Afstemming van de kauwdruk op de momentane eigenschappen van het voedsel en registratie van de konditie van het voedsel, zodat slikken op het juiste moment begint, zijn bijvoorbeeld noodzakelijk voor een efficiënt verloop van het kauwproces. Of proprioceptoren in de spieren, dan wel zintuigen in de weefselflappen die tussen tanden en kauwplaat uitsteken en hen waarschijnlijk schoonvegen, hierbij een rol spelen is onbekend. Smaakknopjes en oligoville cellen hebben mogelijk mechanoreceptieve funkties en zijn de enige sensoren die vooralsnog in de mond-keelholte van de karper struktureel werden aangetoond (hoofdstuk 3).

Over funktionele verbindingen tussen proprioceptoren en het centrale zenuwstelsel is alleen voor de ademhalingsregulatie een en ander bij de karper bekend (Ballintijn, 1972; Luiten, 1977).

Welke mogelijkheden en beperkingen heeft de karper om de beschikbare voedselbronnen te benutten?

Naar de aard van het voedsel worden algemeen carnivore, herbivore, detritivore en omnivore vissen onderscheiden (Nikolsky, 1963). Dat de vis zich niet in een dergelijk schema laat ordenen wordt overtuigend geïllustreerd aan de Afrikaanse *Haplochromis* soorten (cichliden) waarin de trofische differentiatie zich zo sterk manifesteert, dat een verregaande opsplitsing van deze trofische hoofdgroepen noodzakelijk is. Ook sterk gevarieerde mengvormen komen voor. Barel (1983) laat voor deze groep zien, dat binnen eenzelfde voedselkategorie de funktionele eisen aan het voedingsapparaat zeer verschillend kunnen zijn (eieren zuigen van de bodem - eieren zuigen uit een bek-broedend vrouwtje), terwijl ook verschillende kategorieën dezelfde eisen kunnen stellen (inwendig transport van zoöplankton en eieren). Het zal duidelijk zijn dat ook de mechanische eigenschappen van het voedsel niet eenvoudig met de vermelde voedselkategorieën overeenkomen (vgl. slak-worm; slak-plantenzaden). Bovendien wordt de darminhoud bij voedseloverovervloed sterk bepaald door het voedselaanbod. Ook het voederen met pellets in de visteelt maakt de vis nog niet tot een gespecialiseerde pelletfeeder.

De efficiency van de voedselopname wordt waarschijnlijk vooral bepaald door de vereiste behandelingstijd ('handling time') en de verhouding tussen bestede en verworven energie. In een situatie van voedselschaarste spelen specialisaties in bouw en gedrag een belangrijke rol. De soortspecifieke komponent in het dieet van de vis wordt waarschijnlijk bepaald door specialisaties voor dát voedsel waarmee ze in efficiency van opname en verwerking boven andere soorten uitstijgt. Zo blijkt de graskarper beter dan de andere vissen in staat planten als voedselbron te benutten. Wellicht speelt de gespecialiseerde bouw van het kauwapparaat hierin een beslissende rol. Het is te verwachten dat specialisaties voor het ene deelproces die voor andere beperkt. Zo vereist de selektie tussen voedsel en niet-voedsel bij de karper een nauwe keelspleet en reduceert daarmee de rol van de keelholte bij het zuigen.

De specialisaties voor deelprocessen in de karper en de beperkingen die hier voor de benutting van het voedselaanbod uit voortvloeien worden voor elk deelproces zo goed mogelijk aangegeven in hoofdstuk 2. Optelling van deze restrikties leidt tot het volgende beeld. Slechts langzame en kleine voedseldelen (< ca. 9% van de lichaamslengte van de karper (SL) in diameter) kunnen worden opgenomen en deze hebben slechts gedeeltelijk tot de kauwholte toegang (< ca. 3% SL). Fijne partikels (< 250 µm) gaan door de kieuwzeef verloren. Taaie en vezelige materialen kunnen slecht worden gebroken, waardoor de efficiënte vertering van plantaardig voedsel sterk wordt beperkt. Dit vernauwt het efficiënt te benutten voedselskala van deze 'omnivore' vis goeddeels tot plantenzaden, macro- en micro-evertebraten (250 µm - 3% SL).

Als voornaamste specialisaties gelden het benutten van harde, brosse en stijve voedselobjekten (plantenzaden, mollusken) en het exploiteren van voedsel dat met bodemmateriaal is vermengd. Uit de literatuur blijkt opvallend genoeg dat de darminhoud van deze euryfage vis soms meer (weliswaar zachte) macrofyten bevat dan verwacht. Gebrek aan ander voedsel kan hier mede oorzaak van zijn.

Deze konklusies strekken zich niet uit tot jonge karpers. Over het verband tussen hun specifieke dieet (vgl. Uribe-Zamora, 1975) en de relatieve groei van de verschillende kopelementen tijdens de kritieke juveniele fase is nog weinig bekend. Het mechanisme van prooivangst in relatie tot de groei wordt momenteel aan juveniele karpers onderzocht (M.Drost).

Ontwikkeling van het protrusie-systeem van de bovenkaak, het palatale en postlinguale orgaan in de keel, en de kauwplaat in de schedelbasis hebben waarschijnlijk door het exploiteerbaar worden van de bodem belangrijk bijgedragen tot het grote succes van de cypriniden in het zoete water. De set van unieke strukturele kenmerken die de cypriniden en catostomiden karakteriseert en ver uiteen liggende delen van de kop omvat wordt vanuit een sterke ontwikkeling van het keelmaalapparaat in een funktioneel verband geplaatst (p.75). In hoofdstuk 3 wordt het plausibel gemaakt dat de karperachtigen zich door specialisatie op de bodem-voedselbronnen uit predatoire voorouders hebben ontwikkeld.

Een verdere uitwerking van ethologische en ekologische aspekten en vergelijking met andere soorten cypriniden zal tot toetsing en verfijning van gestelde hypotheses en konklusies bijdragen. Dit zal ook tot meer inzicht leiden in de trofische segregatie van verschillende soorten, die naast elkaar in één levensgemeenschap voorkomen.

Samenvatting en konklusies

In dit proefschrift worden de onderdelen beschreven van het proces van voedselopname en -verwerking bij de karper (*Cyprinus carpio* L.), de bouw van de lichaamsdelen die hierbij betrokken zijn en de funkties van de afzonderlijke deelprocessen en strukturen. Het doel is de samenhang tussen de architektuur van de karperkop en zijn funkties te bepalen en inzicht te geven in het naast elkaar bestaan van verschillende vissoorten in een levensgemeenschap door naast de specialisaties van deze vis voor bepaalde voedselsoorten de daaruit voortvloeiende beperkingen voor andere vast te stellen.

- De cypriniden of karperachtige vissen bezitten tot keelkaken gemodificeerde vijfde kieuwbogen, die tegen een kauwplaat worden bewogen door oorspronkelijke kieuwboogspieren. De bek draagt geen tanden. Een maag ontbreekt. De bovenkaak van de karper is uitstulpbaar, waardoor een ronde zuigmond gevormd kan worden. De mond- en kieuwholte kunnen sterk in volume veranderen. De keelholte wordt vrijwel geheel ingenomen door een dorsaal gespierd palataal orgaan. Ventraal ligt het postlinguaal orgaan en de kieuwzeef. Het oppervlak van keeldak en bodem is bijna geheel bedekt met smaakknoppen (tot 820/mm^2) en slijmcellen. De spleetvormige keelholte kan maar zeer beperkt in volume variëren, in tegenstelling tot bij de meeste andere vissen. Het bij dit pharyngeaal systeem behorende hersencentrum ligt in het verlengde merg en benadert in omvang de grote hersenen.
- De rol, die deze structuren bij de opname en verwerking van voedsel vervullen is bij de karper onderzocht m.b.v. gewone- en röntgenfilmopnamen van levende vissen. Meting van aktiviteit in de bij dit proces betrokken spieren werd, synchroon op negen kanalen, gekoppeld aan deze bewegingsstudies. Het voedsel bestond uit visvoerpellets, graan, wormen, watervlooien, tubifex en bodemmateriaal vermengd met tubifex. Door impregnatie van voedsel met $BaSO_4$ werd de weg van het voedsel op de röntgenfilm zichtbaar gemaakt. Struktuur onderzoek geschiedde op macroscopisch, lichtmicroscopisch en scanning-electronenmicroscopisch niveau.
- Elk eetproces blijkt uit een wisselend aantal stereotype bewegingspatronen opgebouwd: deeltjes opname (particulate intake) of slokken (gulping), selektie tussen eetbare en niet-eetbare delen (wassen, positioneren of terugspoelen), verzamelen van het door de kieuwzeef gevangen materiaal, transport van voedsel en het vullen van de kauwholte, plet- en/of maalbewegingen afgesloten door slikken. Monsteren van de bodem en spuwen worden apart beschouwd.

- Het moment en de mate en snelheid van bekopening, protrusie van de bovenkaak, opening van de kieuwdekselklep, en van de volumeveranderingen in mond-, keel- en kieuwholte bepalen samen het effect van elk patroon. Opname, selektie, transport en kauwen stellen verschillende eisen aan de kop en zijn alleen los van elkaar effektief uitvoerbaar.
- De opbouw van het voedselopname proces uit de genoemde stereotype bewegingspatronen varieert met de grootte, aard en verontreiniging van het voedsel. De totale hanteertijd van een voedseltype, te meten aan het electromyogram, varieert vooral door herhaling van voor dát voedsel specifiek vereiste bewegingspatronen.
- De kwantitatieve verdeling van smaakknoppen, slijmcellen, clubcellen en spiervezels is in mond- en keelholte gemeten. Op grond van deze verdeling en andere morfologische kenmerken worden zes gebieden in de mond-keelholte onderscheiden en aan de deelprocessen voor voedselopname en -verwerking gerelateerd. Scanning E.M. beelden worden gegeven van gewone epitheelcellen met microrichels, verhoornde cellen, slijmcellen, smaakknoppen en oligoville (sensorische ?) cellen.
- Gerichte opname van deeltjes (particulate intake) wordt bereikt door een snelle en volumineuze zuigbeweging, opgewekt door vergroting van de mond- en kieuwholte. De bovenkaken worden hierbij vooruitgestulpt (protrusie) waardoor een snelle en naar het voedsel gerichte waterstroom (ca. 60 cm/sec.) ontstaat. 'Gulping', het langzaam en ongericht opslokken van water met gesuspendeerd voedsel, geschiedt door vergroting van alleen de mondholte. Door het naar beneden stulpen van de bovenkaak sluit de vis de suspensie in. Kompressie van de mondholte perst de suspensie door de kieuwzeef. De energie nodig voor een slokbeweging zal beduidend minder zijn dan die voor deeltjes-opname.
- Grote dichtheden clubcellen, die in de huid een voor cypriniden kenmerkende alarmstof produceren, komen ook en alleen in de mondholte voor. Hun alarmfunktie op deze plaats wordt in twijfel getrokken.
- Selektie vereist het vasthouden van eetbare en de afvoer van niet eetbare deeltjes. Uit electromyogrammen en electrische stimulatie valt af te leiden dat deze scheiding plaats vindt door de vorming van bultjes op het palataal orgaan. Tussen dit orgaan en de kieuwzeef zullen eetbare delen worden vastgezet; niet-eetbare worden weggespoeld. De complexe bouw van het palataal orgaan, de bijna maximale dichtheden van smaakknopjes en de cyto-architektuur van het hierbij betrokken regelcentrum in de achterhersenen wijzen op een groot scheidend vermogen. De brede spleetvormige keelholte waarborgt een groot kontaktoppervlak tussen dak en bodem maar beperkt tevens haar rol bij het zuigen.

- De vergroting van de mondholte door protrusie met gesloten bek speelt bij selektie een belangrijke rol door het mengsel van voedsel en niet-voedsel in de mondholte te resuspenderen. Door afwisselend expanderen en komprimeren van de mondholte wordt een op en neer gaande stroming door de kieuwspleet en kieuwzeef bereikt. Voortdurende herhaling van 'gesloten protrusie' en selektie leidt tot steeds verdere zuivering van het voedsel. Gesloten protrusie speelt ook een rol bij het positioneren van grotere delen en bij het verzamelen van het filtraat uit de kieuwzeef.
- Slijm met lage viskositeit (sialomucinen) wordt aangetroffen in de voorste delen van mond- en keelholte. Het dient mogelijk voor de verlaging van de stromingsweerstand langs de wand en beschermt het onderliggende weefsel. Achterin de keelholte waar aggregatie van voedseldeeltjes voor verder transport verwacht moet worden, vinden we cellen die veel en sterk viskeus slijm (sulfomucinen) produceren. In slijm gevat voedsel wordt via een gekombineerde peristaltiek in palataal en postlinguaal orgaan naar en in de kauwholte getransporteerd.
- De keelkaken zijn onderling beweeglijk in spierlussen opgehangen en door een glij-koppeling met de kieuwkorf verbonden. Voedsel wordt geplet en/of gemalen tussen de keeltanden en de verhoornde maalplaat aan de schedelbasis. Bij het maalproces kunnen mais en gerstekorrels worden verbrijzeld met een buiten het aquarium hoorbaar geluid.
- Aangetoond is dat de rugspieren via schedelrotatie belangrijk bijdragen aan de plet- en maalkrachten. Via de schoudergordel dragen ook de buikspieren hun krachten met een grote momentarm op de keeltanden over. De konstruktie van het maalapparaat is er op gebouwd hoge kauwdrukken te produceren en te weerstaan.
- In tegenstelling tot deze 'kracht-spieren', zijn de direkt op de keelkaken aangehechte spieren meer 'stuur-spieren'. Zij richten en stabiliseren de beweging van de keelkaken om vier anatomische assen.
- De werking van het maalapparaat met de beweeglijke schedel maakt een starre keten van 'gehoorbeentjes' tussen zwemblaas en het inwendige oor onmogelijk. De vele beentjes van Weber en hun loop langs de rotatie-as van de schedel lijkt daarom een konstruktieve noodzaak.
- Slikken geschiedt door kompressie van de kauwholte, waarbij afsluiting van haar toegang door het palatale en postlinguale orgaan het transport naar de slokdarm richt. Beweging van de keelkaken ondersteunt dit transport.
- Het voedselopname-apparaat van de karper blijkt gespecialiseerd voor het verwerken van kleine voedseldelen (van 250 µm tot ca. 3% van de lichaamslengte) en voor voedseldelen die vermengd met oneetbare delen voorkomen. Klein en

hard voedsel wordt effektief verwerkt (zaden, mollusken). Snelle, grote en spartelende prooien en grote platte delen van planten kunnen niet effektief verwerkt worden. Dus ook de 'omnivore' karper is door specialisaties voor bodemvoedsel gelimiteerd in het benutten van andere typen.

- De unieke set van kenmerken die cypriniden karakteriseert kan worden uitgelegd als aanpassing aan het leven en zich voeden op de bodem. Het kauwapparaat speelt hierin een centrale rol.
- Dit onderzoek biedt een nieuw startpunt voor onderzoek naar de regulatie van de voedselverwerking en voor vergelijkend onderzoek aan inheemse karperachtigen als brasem, blankvoorn, zeelt e.a.. Door inzicht in de mogelijkheden en beperkingen van het voedselopname en -verwerkingsapparaat kan duidelijker worden aangegeven welke de plasticiteit van de vis in de benutting van verschillende voedseltypen is. Deze plasticiteit bepaalt mede de overlevingskans van de betreffende vissoort in situaties met een beperkt voedselaanbod en daarmee de konkurrentiepositie van de soort. De verkregen kennis draagt zo bij tot het voorspellen van het effekt van veranderingen in het milieu op de trofische interakties en de samenstelling van de visfauna.

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HOOFDSTUK 2

FOOD HANDLING IN THE CARP (*Cyprinus carpio* L.), ITS MOVEMENT PATTERNS, MECHANISMS, AND LIMITATIONS.

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SUMMARY

The oro-pharyngeal feeding mechanism of the carp was analyzed as a case study for cyprinids. Light and X-ray cinematography combined with electromyography allowed a detailed analysis of the external and internal events during processing of the following food types: radiopaque pellets, earthworms, barley, tubificids, cladoceran suspensions and food-soil mixtures. In feeding twelve functional patterns of headmovements and activities are distinct. Particulate feeding and gulping for intake; rinsing, repositioning or back-washing and spitting for selection; recollection from the branchial sieve, transport, loading of the teeth, crushing, grinding and deglutition. The mechanism of each single pattern is discussed. The expansion mechanism of the head is versatilely used in food handling by the adequate timing of upper jaw protrusion, volume changes in the oral, buccal and opercular cavities and of the opening of the mouth and opercular valves. Muscular cushions in the pharyngeal roof (palatal organ) and floor (postlingual organ) play a prominent role in internal selection between food and non-food and in transport. They permit postcapture selection of food. Protrusion of the upper jaw is crucial in food processing and serves different functions in particulate intake, gulping and in selection between food and non-food particles inside the pharynx.

The effects of the separate movement patterns on the food and the implicated restrictions for processing different types of food are discussed. Tentative limits are set to the feeding on the available food types in the environment. The feeding apparatus appears to be ill constructed for exploiting very small particles ($<250\,\mu m$), plant and other materials of fibrous context. Only slow and immobile food particles with a diameter up to ca. 3% of the carps body length are effectively processed. The carp appears to be a generalist in its diet with specializations for the exploitation of food and non-food mixtures from the bottom, even if the contained food is of considerable density and hardness.

The distinct elements of feeding behaviour are considered to be stereotyped action patterns. They are released and steered according to the actual size, distribution, consistency and contamination of the food and integrated into varied feeding sequences. Different food types require different 'handling times' due to the varied repetition frequency of specific patterns within one feeding sequence, related to the properties of the food. Probing and spitting do not lead to ingestion and are employed in search and rejection. Protrusion with closed mouth appears to be a core pattern in food handling as it is basic to repositioning and back-washing during purification of food. It will also serve recollection of retained food from the branchial sieve.

Protrusion and the palatal and postlingual organs in this lower teleost are discussed in relation to the hypertrophy of the pharyngeal masticatory apparatus, the recruitment of body power for mastication and to the evolutionary loss of toothed upper pharyngeal transporting bones. Protrusion as well as these sensory muscular organs are basic to the substrate feeding habits for many cyprinoids.

The significance of functional morphology, ethology and ecology for the study of limitations in the exploitation of available niches is emphasized.

Contents

INTRODUCTION

Abundant reports exist on feeding structures, pointing to their adaptive character. Paradoxically, few experimental evidence assess their role in feeding.
Over the last decades gradually more detailed analyses of function have been performed in fish to supply evidence for such feeding adaptations (Alexander, 1969; Osse, 1969; Liem, 1973; Lauder, 1983). The specializations for food intake have been focal points for functional anatomists but an overall theory providing testable hypotheses was lacking. A recent model for suction-feeding (Muller, Osse and Verhagen, 1982; Muller and Osse, 1984; van Leeuwen and Muller, 1984) presents the options which a fish has to manipulate the flow of prey and water into the mouth. However intake is only a first step in food processing, especially in benthic feeding as employed by cyprinids. Enquiries into the functional aspects of dentition and food processing have been limited in scope and are largely descriptive (Hyatt, 1979). The need to develop precise, experimentally based assessments of the mechanisms controlling food exploitation in fishes is apparent. The concealed character of food processing, occurring inside the complex orobranchial cavity, largely obstructed a detailed analysis of food handling once it is entered the mouth.

This paper studies the external and internal food processing in the carp. X-ray cinematography combined to electromyography recently allowed a detailed functional analysis of pharyngeal mastication in the carp (Sibbing, 1982). Similar techniques are applied here to analyse movement and activities of the head parts, and the path followed by particles from intake to deglutition. We seek for distinct movement patterns in feeding behaviour, to analyse their mechanism and to explain their effect for food handling. This knowledge is used to describe optimizations and restrictions of the feeding apparatus to exploit particular food types in the environment.
The following feeding elements are distinct for the carp. Search and detection of food, intake, gustation and selection between food and non-food, recollection of food from the branchial sieve, transport, mastication, deglutition and digestion. Each single species will have its specific set of structures and actions contributing to the specificity of its feeding behaviour. Details of the oro-pharyngeal lining and their role in food processing is presented in a concurrent paper (Sibbing et al., 1984).

Selective pressure acts through the efficiency of behaviour. Structures and their actions allow as well as limit the exploitation of the environment by the fish. The mechanisms of food processing in cyprinids should be understood to determine their efficiency. Limits thus set on the usable food are important to distinguish

the exploitable niches in the aquatic ecosystem.
Such knowledge is required when studying fish-food and fish-fish interactions or even exploiting them in management and control of natural, or artificial, fish resources. Cyprinids have a high impact on aquatic systems and fisheries.

The *Cyprinidae* assemble the largest (freshwater) fish family with a wide ecological and trophical differentiation. Contrary to non-cyprinoid teleosts cyprinids lack teeth on the jaws but instead have strong pharyngeal teeth impacting on a cornified chewing pad (Sibbing, 1982). They include many bottomfeeders which take portions of soiled food. The actual separation between food and non-food proceeds in the orobranchial cavity.

Stimulating studies on the buccopharyngeal feeding mechanism in cyprinids (Girgis, 1952; Matthes, 1963; Robotham, 1982) lack functional data to verify hypotheses. For example, the size-selective effect of the branchial sieve with its gill rakers is generally agreed upon (Zander, 1906; Iwai, 1964). The detailed mechanism of size-selection and its efficiency is however still unclear.

The omnivorous common carp (*Cyprinus carpio* L.) is a practical choice for this study. Extensive data are available on its feeding habits and also from other disciplines, affording a wide platform of knowledge necessary for relating the structures of the feeding apparatus to the usable food in its habitat.

MATERIALS AND METHODS

All mirror-carps (*Cyprinus carpio* L.) hatched in our laboratory culture and were selected between 28 and 35 cm SL for the experiments. Records of the feeding events were made at room temperature (± 20°C). Care was taken to maintain the proper pH and nitrite content of the water.

Details of operation techniques, the experimental set-up, electromyography and simultaneous X-ray cinematography have been described in a previous paper (Sibbing, 1982). Shortly summarized, electrodes and radiopaque markers were inserted in the anaesthetized carp which had been trained to feed in a small cuvet with circulating water. The cuvet keeps the head of the animal within the X-ray beam and parallel to the image-intensifier. It furthermore restricts the volume of water which would otherwise absorb most X-rays and thereby cause the image of the carp to be vague or even absent. Platinum markers allowed accurate measurements of the movements of the jaws, the orobranchial roof and floor and many other structural components of the head (cf. Plate I).

Light-movies were taken from a large tank (80x50x40 cm) using a 16 mm Teledyne DBM 54 camera at film speeds between 24-60 frs/sec. This allowed sustained recording of feeding behaviour over prolonged periods and at the same time permitted detailed analysis of the single frames. Feeding movements in the omnivorous carp are slow compared to those of predaceous fish. The procedure for measuring was based on exterior marks and contours of the fish in simultaneously taken lateral and ventral views (cf. Plate I).

About seventy feeding performances, from five experiments, were studied with a single-frame projector (Analector 6, Oldelft). Three representative examples of each of the described movement patterns were measured in detail. These patterns were recognized in other frame sequences, like those depicted in this paper (cf. Plate II). From the X-ray movie one illustrative food handling sequence was measured in detail over more than 15 seconds (cf. Fig. 2). Many short actions were analyzed from other scenes. Eight EMG-experiments, often combined with movies, verified the role of palatal and postlingual organs in feeding. Representative recordings were selected for illustration. The variable time course of the feeding sequence renders the averaging of patterns inadequate. Movement patterns are named after their role in food handling. Note that one type of movement (e.g. closed protrusion), due to its different role in handling different food types, may belong to several patterns (e.g. repositioning, backwashing and recollection. cf. Fig. 8).

Pressures in the opercular cavities were recorded in a series of feeding sequences from a single experiment. This was done with Millar micro-tip catheter pressure transducers (van Leeuwen and Muller, 1983). The pressure is expressed in pascals (1 kPa corresponds to ca. 10 cm water).

Carps were offered foods differing in location, dispersion, movement, size, shape, consistency and soilure viz: fine and coarse pellets (diameter resp. 0.5 and 5 mm), barley, earthworms (cleaned or slightly soiled), tubificids (lumps or mixed through pond soil) and cladocerans (*Daphnia magna*). During the experiments combining electromyography and X-ray cinematography, coarse radiopaque ($BaSO_4$ impregnated) pellets provided a dynamical view of the internal processing by carp.

RESULTS

Subdivisions of the headgut (Fig. 1)

Different parts of the headgut perform their own particular movements during feeding. A clear distinction between them is a prerequisite for correct interpretation of the results. Therefore the nomenclature of the compartments is shortly given (Fig. 1).

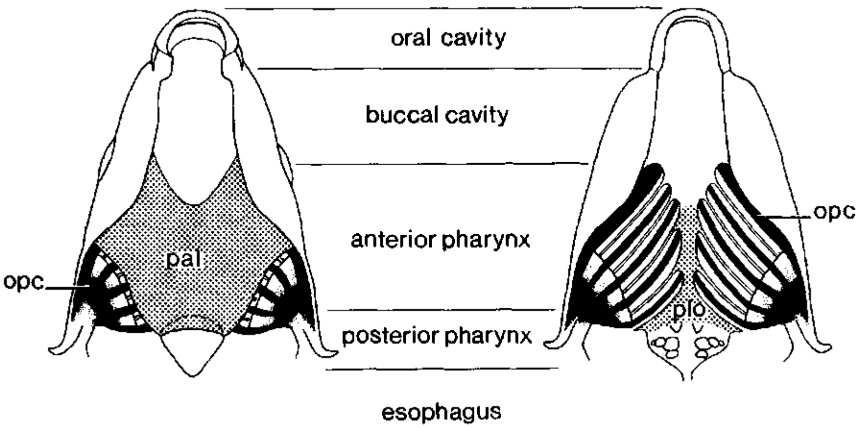


FIG. 1. Nomenclature of the cyprinid headgut. Palatal organ (pal) in the roof and postlingual organ (plo) in the floor of the anterior pharynx are shaded. The opercular cavity (opc) is black. Further explanation in text.

The **oral cavity** extends between the lips and the articulations of the lower jaw. Depression of the lower jaws thus lowers the oral floor completely (cf. Plate I). The **buccal cavity** lies between the lower jaw-articulations and the first branchial slits. The buccal floor is depressed by lowering of the basal hyoids. The **anterior pharynx** is bordered by the gill arches and a common synonym reads branchial cavity. It has a muscular roof, the palatal organ. The midventral floor between the arches is covered by a muscular pad, the postlingual organ. The **posterior pharynx** lies between pharyngeal teeth and chewing pad and is often referred to as chewing cavity. Caudally it converges into the narrow **esophagus.** The pyloric sphincter separates the esophagus after short distance from the wide intestinal bulb (cf. ib Fig. 12). The **opercular cavities** connect the anterior pharynx with the exterior of the fish. They contain the respiratory filaments projecting from the branchial arches.

Twelve movement patterns compose the food processing sequences.

Upper and lower jaw movements, depression of the buccal and pharyngeal floor, and the events of the food were measured in X-ray movies of carps feeding on radiopaque ($BaSO_4$ impregnated) pellets. Note that the distances measured (Plate I) do not correspond directly to the orobranchial lumen between the fleshy parts. For comparing respiration and mastication at the same time activities were recorded in the levator operculi muscle (LOP) depressing the lower jaw (Ballintijn,

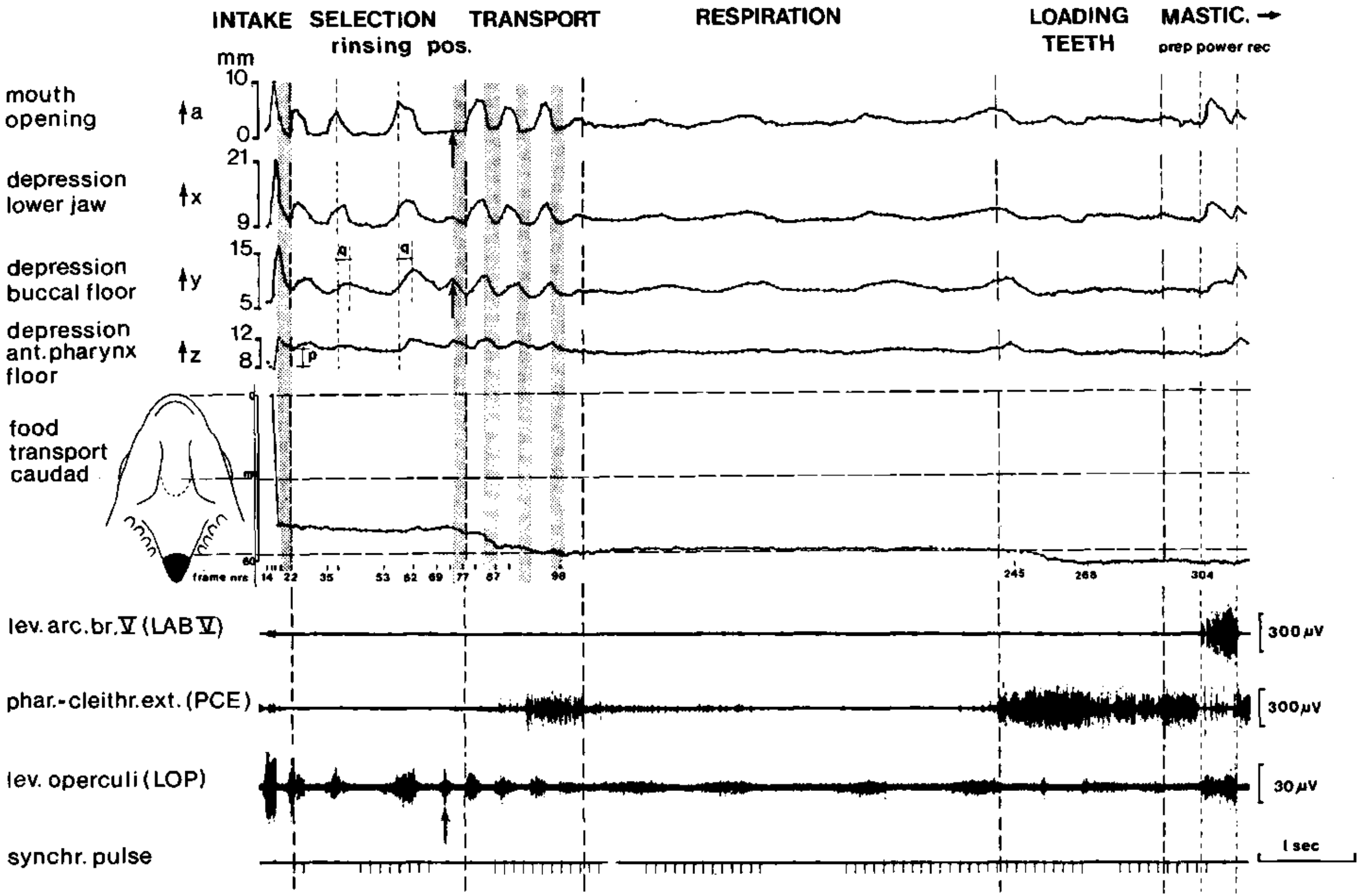


FIG. 2. Particulate feeding. Head movements, food transport and synchronous reference-EMGs (see text) during feeding on a radiopaque pellet in the carp, measured from an X-ray movie (24 frs./sec.). Frame numbers refer to their prints in Plate II and IV; a, x, y and z are indicated in Plate I.

Seven successive movements patterns are distinguished in this particular sequence viz. intake, rinsing and posi- tioning, transport to the chewing pad, interrupted by respiration, loading of the teeth and crushing. Note that volume changes in the anterior pharynx (trace 4) are small compared to those in the orobuccal area (traces 1-3). The arrows mark protrusion with closed mouth, accompanied by a characteristic short burst in the LOP muscle (i.e. closed protrusion, cf Plate III). Further discussion in the text.

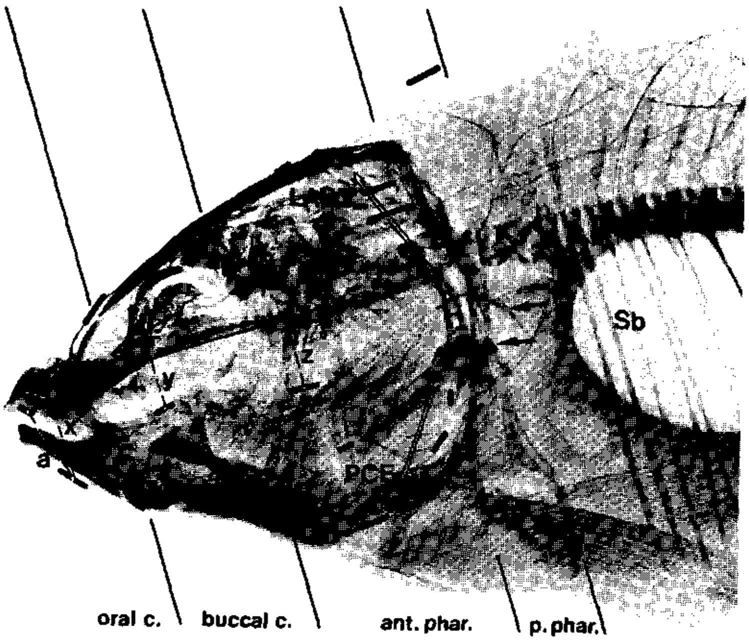


PLATE I. X-ray picture of the common carp. Subdivisions of the oro-pharynx correspond to Fig. 1. Note the metal markers inserted into the skull, jaws, buccal floor, anterior pharyngeal floor, pectoral girdle, opercula and pharyngeal jaws to allow detailed analysis of movements. The pharyngeal jaws and teeth as well as the opposed projection from the skull (solid arrows) accomodating the chewing pad are conspicuous in front of the swimming-bladder (sb). Open arrows indicate the action lines of two pharyngeal jaw muscles connecting them to the skull (LAB V) and pectoral girdle (PCE); a, x, y and z indicate the distances measured in the X-ray frames (cf. Fig. 2).

Parameters measured from the light-movies (cf. Plate II) correspond to the distances between the surface-mark on the frontal skull and the tip of the upper jaw (protrusion), between the tips of lower and upper jaw (mouth opening), between the frontal skull and the lower jaw tip (depression lower jaw), between the sharp circumorbital edge and the external skin mark below the hyoid (depression buccal floor) and, in ventral view, between the caudal edges of left and right opercula (opercular abduction).

1969) and in two muscles characteristic for the time course and effort during mastication (Sibbing, 1982). These were the levator arcus branchialis V muscle (LAB V) effective in crushing and grinding during the power stroke, and the pharyngocleithralis externus muscle (PCE) reflecting the preparatory and recovery stroke (Plate I). Similar and opercular movements were measured from the light movies in lateral as well as in ventral view.

Combination of data from the interior and exterior of the fish and EMG results show twelve distinct movement patterns in feeding, applied in dependence of the type and condition of the food. a) Food intake proceeds by **particulate feeding** or **gulping**. b) Selection is effected by different patterns, meanwhile tasting the particles. It proceeds by **rinsing** when a fixed particle is flushed with a rostro-caudad flow of water. Closed protrusion may result in **repositioning, back-washing** or **recollection** of particles. Unwanted particles may be ejected by **spitting**. c) **Transport** indicates movement of selected food from the anterior pharynx to the chewing cavity. **Loading** finally brings the food between teeth and chewing pad. d) Mastication involves **crushing** and **grinding.** e) **Deglutition** is the passage of ground food into the digestive tract.

As size and consistency of a pellet allow a clear distinction of the subsequent patterns in food processing, contrary to long or suspended food, such a pellet-sequence is described in detail referring to the X-ray results from Figure 2. Each movement pattern is separately depicted in graphs and a series of frames (Plate II-VI), and characterized in Table 1 (pag. 46).

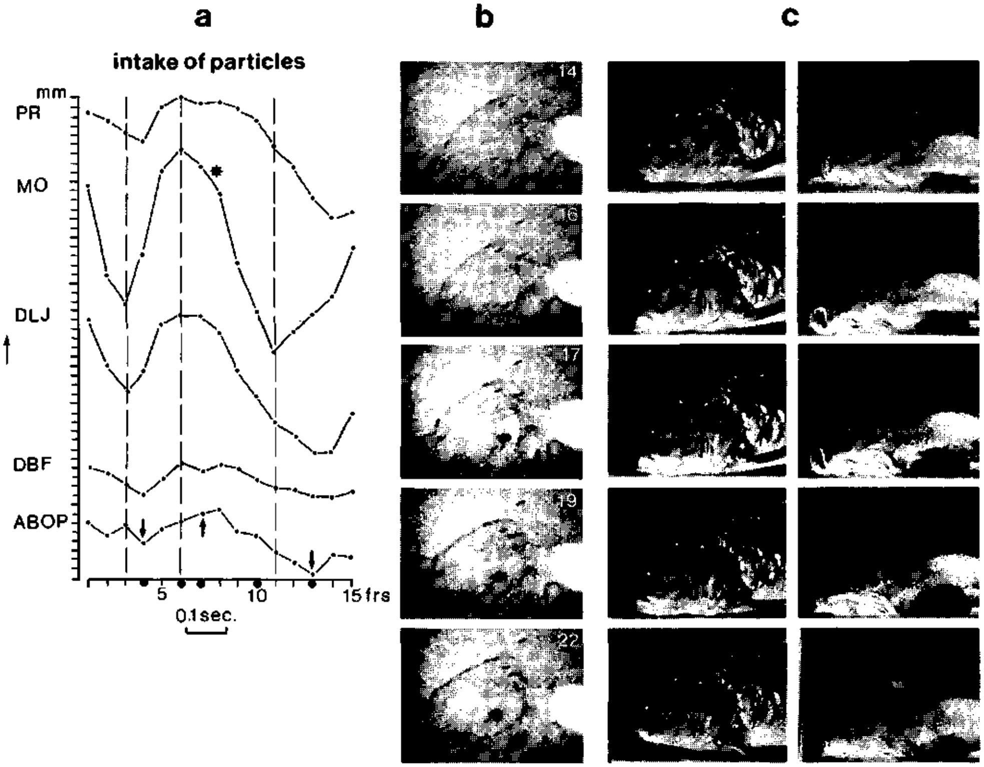


PLATE II. Particulate feeding. Food intake movements of the carp and the internal path of the (black) particle. (IIa) Movement graphs of the headparts. (IIbc) Corresponding internal and external views from two other particulate intakes. Numbers at the X-ray frames (24/sec.) correpond to Fig. 2. The approximate timing of the others has been indicated (●) at the frame-scale in the graph.

Combination of data shows that food enters (*) the widely opened mouth after depression of the orobuccal floor and opercular abduction have caused a suction flow (IIa. frs. 4-8). The opercular valves only open (↑) once oral compression starts. Note that protrusion is maintained during mouth closure (IIa frs. 6-10). The radiopaque food is immediately trapped in the narrow pharyngeal cavity (IIb).

PR	protrusion upper jaw	MO	mouth opening	DLJ	depression lower jaw
DBF	depression buccal floor	ABOP	abduction opercula		

Particulate intake (Plate II)

Offering carps large particles elicits 'particulate feeding', characterized by the aiming of the fish to the food (cf. Janssen, 1976) and the following features.

Fast intake (ca. 60 cm/sec.) occurs at sudden expansion of the fully compressed oro-pharyngeal cavities (Fig. 2). The large particle is finally trapped in the still narrow horizontal slit between roof and floor of the anterior pharynx (cf. Plate IIb). The large size of the pellet even obstructs its full recompression (Fig. 2, mark p). The levator operculi (LOP) muscle is highly active during fast depression of the lower jaw. The combined action of the LAB V and PCE muscles support expansion by moving the posterior wall of the pharynx caudad (Sibbing, 1982) while the pectoral girdle is slightly retracted (2°; not depicted).

Analysis from the exterior of the fish (Plate IIac) shows that lower jaw depression initiates mouth opening, later aided by protrusion of the upper jaws. Within short time depression of the buccal floor, elevation of the cranium (ca. 10°) and abduction of the opercula cause the food to be sucked into the widely opened mouth (Plate IIa,*). The closed opercular and branchiostegal valves open once lifting of the lower jaw reduces the gape of the mouth. Protrusion maintains during this increasing oral compression until the mouth has almost closed.

The negative opercular pressures measured during intake of particles in the carp (5-9 kPa) lie in the same range as recorderd in the buccal cavity of goldfish and orfe (resp. maximal 9 and 10.5 kPa; Alexander, 1970).

Selection - **rinsing** (Plate IVa)

The trapped food pellet is subsequently gustated and rinsed (Fig. 2) by repetitive pumping of water through the orobranchial cavity. Protrusion does not occur (cf. Plate IVa) and, contrary to food intake, mouth opening amply preceeds buccal expansion (Fig. 2; compare trace 1 and 3 at intake and rinsing, mark q). Due to this delay the suctionflow will be slow, but because of its high amplitudes voluminous compared to respiration. Note the steady state in the anterior pharynx as it fixes the pellet (Fig. 2; traces 4,5).

Selection - **repositioning** and **back-washing** (Plate III)

A characteristic fast protrusion of the upper jaw with closed mouth (Fig. 2; arrows) follows rinsing. The fully compressed orobuccal cavity is expanded by conspicuous depression of lower jaw and buccal floor, while simultaneously extensive protrusion of the upper jaws keeps the mouth closed (Plate IIIa,c). This *'closed protrusion'* movement creates a rostrad flow through an anterior volume increase,

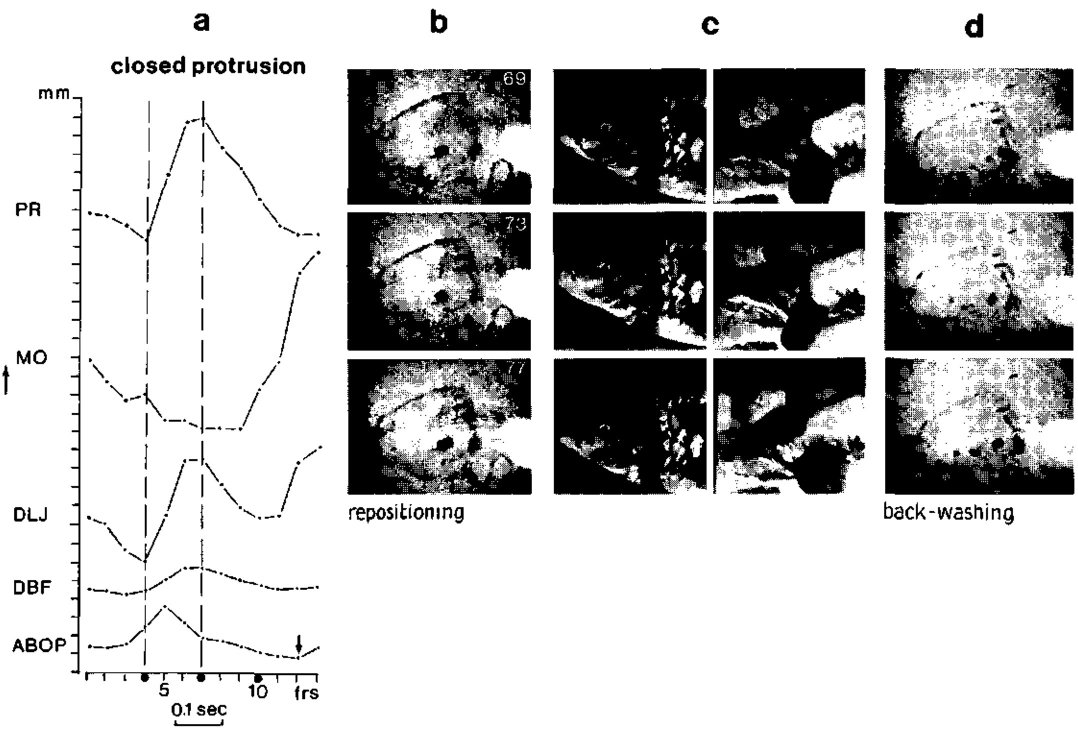


PLATE III. Closed protrusion and its effects on the internal path of the food. (a) Movement graphs. (bcd) Corresponding internal and external views from three other closed protrusions illustrating its role in repositioning (b) and back-washing (d) of food. Frame numbers in IIIb (24/sec.) correspond to Figure 2. The approximate timing of the others has been indicated (●) at the frame-scale in the graph.

Orobuccal expansion occurs by depressing the lower jaw and buccal floor, while protrusion of the upper jaws keeps the mouth closed (frs. 4-7). This causes a rostrad suction flow from the open opercular slits (arrow marks closing), repositioning (b) or even washing the particles rostrad (d). Opercular adduction supports this rostrad flow (frs. 5-7). Abbreviations as in Plate II.

while at the same time water enters through the early opened opercular slits. It effects a **repositioning** of the food (Plate IIIb) set free by slight expansion of the anterior pharynx (Fig. 2). It is evident from other X-ray scenes that closed protrusion often **washes back** food particles from the posterior area of the pharynx to the orobuccal cavity (Plate IIId). In the second half of buccal expansion (Plate IIIa, frs. 5-7) the opercula even support the rostrad flow by adduction. Eventually orobuccal and opercular compression reverse the flow and expel the water only through the opercular slits (frs. 7-10). Particles may now have been flushed through the branchial sieve or been retained in the pharynx. In such a way closed protrusion forms also part of the mechanism for selection between food and non-food leading to purification (see discussion). Closed protrusion occurs frequently, but irregularly during food processing and is characteristically accompanied by a short burst of activity in the LOP muscle, fastly depressing the lower jaw. Ballintijn et al. (1972) reported such jaw movements in the carp and supposed that the reversed flow over the gills permitted the fish to breath during food processing, without loosing the food through its mouth. The irregular frequency of closed protrusion and the simultaneous repositioning of food, occurring more frequent as the food is less manageable or more soiled, renders its significance for respiration doubtful.

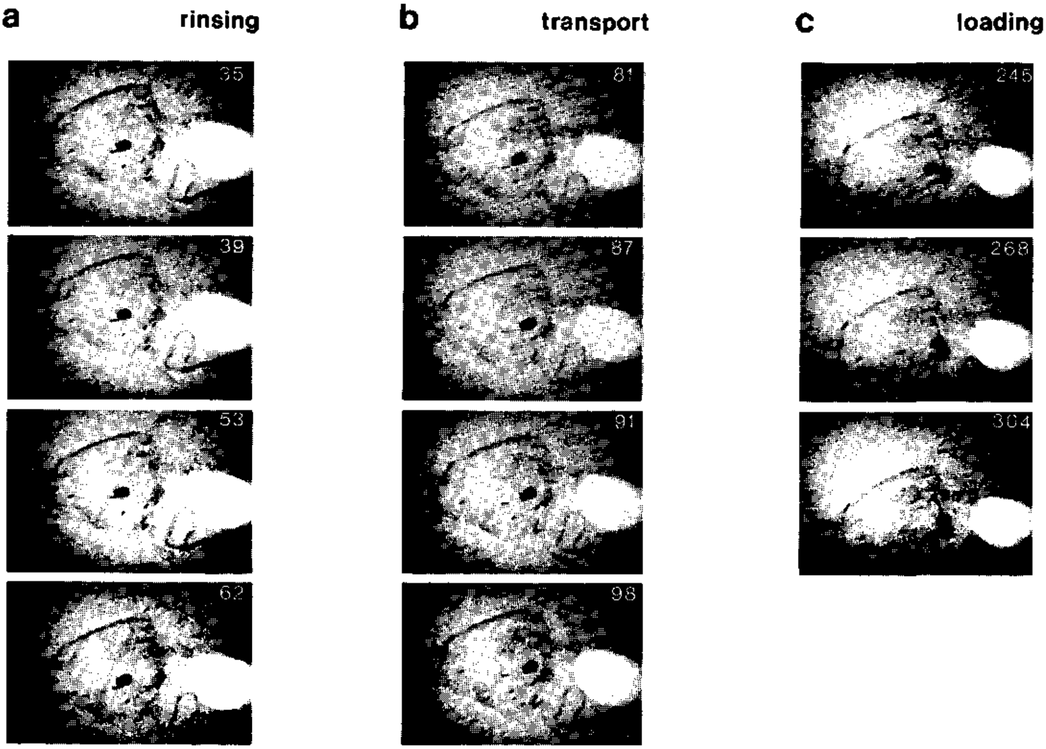


PLATE IV. Rinsing, transport and loading of food on the pharyngeal teeth in the carp, depicted from X-ray movies (24 frs./sec.). At rinsing (IVa) alternatively compressed and expanded stages of the head show the bucco-opercular pumping causing a rostro-caudad flow of water that cleans the food, fixed between pharyngeal roof and floor. Protrusion hardly occurs. Transport of food (IVb) proceeds at compression of the orobranchial cavity and simultaneous expansion of the chewing cavity. Palatal and postlingual organs propel the food by a caudad peristaltic wave (cf. Fig. 3a). Loading of the chewing cavity (IVc) proceeds similarly during full contraction of the anterior pharynx and wide expansion of the chewing cavity. Frame numbers (24/sec.) correspond to those in Figure 2.

Transport (Plate IVb)

Food transport towards the chewing cavity proceeds slowly (ca. 2-3 cm/sec.) (Fig. 2). The actual transport of the large pellet occurs during the compressive phases of pumping movements. More generally, transport proceeds without such pumping and is effected by the palatal and postlingual organs only (cf. Fig. 3a), as discussed later. The chewing cavity is at the same time moderately expanded (Plate IVb). Transport is a more regular movement pattern than selection. A period of quiet respiration may interrupt the sequence of feeding actions, like in Fig. 2. The food is then hold at the entrance of the chewing cavity.

Loading (Plate IVc)

The final transport phase is called loading as it is characterized by manoeuvring the food between pharyngeal teeth and chewing pad into the fully expanding chewing cavity, as appears from the X-ray frames (Plate IVc). The sustained high activity in the PCE muscle (Fig. 2) indicates depression and abduction of the pharyngeal teeth (Sibbing, 1982). Meanwhile the orobranchial cavity remains fully compressed. During loading hardly any external head movements are observed, thus stressing the role of the palatal and postlingual organs (see below).

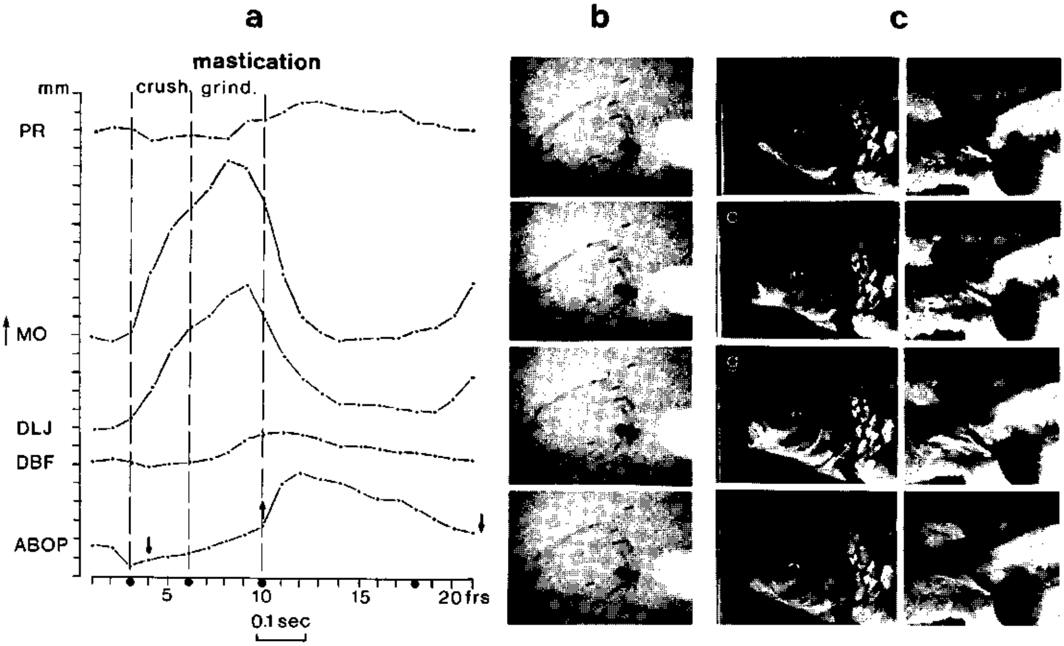


PLATE V. Mastication of pellets in the carp. (a) Movement graphs. (bc) Corresponding internal and external views of two other masticatory cycles. Note that the pellet is successively crushed (c) and ground (g). Note also the terminal mouth, the minor role of protrusion and the elevation of the skull in grinding. The approximate timing of the frames (24/sec.) has been indicated (●) at the frame-scale in the graphs.

These data show that during the crushing phase of the power stroke the buccopharyngeal floor remains still adducted. In the grinding phase the orobranchial floor is extensively depressed and the mouth fully opened, without causing high negative pressures (0.5-1 kPa). Opercular abduction lags behind mouth opening. Overall compression marks the recovery stroke (Plate Va, frs. 10-18). Arrows mark opening (↑) and closing (↓) of the opercular valves. Abbreviations as in Plate II. For further explanation see text.

Mastication: **crushing** and **grinding** (Plate V)

Loading of the teeth is immediately followed by a series of masticatory cycles, which are best characterized by the repetitive bursts of activity in the LAB V muscle effecting the power stroke (Fig. 2). In the crushing phase of the power stroke (Plate V, frs. 3-6) the buccal cavity is fully compressed, whereas grinding (frs. 6-10) requires extensive expansion of the head (Sibbing, 1982). The restrictions which such vigorous movements impose on other functions are discussed later. During mastication of a large pellet the mouth opens widely with hardly or no protrusion. A corresponding activity in the LOP muscle is evident (Fig. 2). The extensive expansion during grinding resembles the events at food intake. Its effect on flow is limited as it proceeds much slower. This was confirmed by pressure measurements in the opercular cavities, which gave a negative water pressure of 0.5-1 kPa during mastication instead of 5-9 kPa during intake. The timing of opercular abduction rather varies and may considerably lag behind mouth opening (Plate IV a). Lifting the cranium and retraction of the pectoral girdle mediate the transmission of forces from the bodymuscles to the masticatory surfaces (Sibbing, 1982). These movements are readily observed in a chewing carp.

Deglutition (Plate VI)

The masticatory train is completed by a deglutition stroke, which is not recognized from the exterior of the fish. Its EMG and movement pattern resembles a masticatory cycle of low amplitude (Sibbing, 1982). During deglutition the ground food is transported from the posterior pharynx into the esophagus (Plate VI, frs. 1-2) and finally passed through the pyloric sphincter into the intestinal bulb (frs. 2-5).

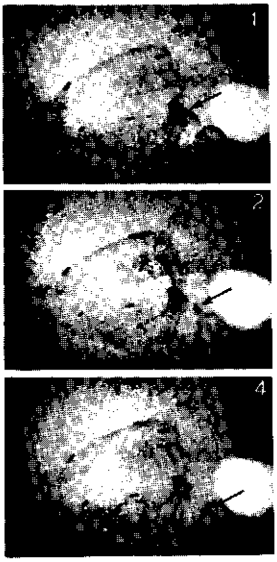


PLATE VI. X-ray frames (24/sec.) visualize deglutition in the carp. Ground food is seen moving from the chewing cavity into the esophagus towards the intestinal bulb (arrows). Small pharyngeal jaw movements play a role in deglutition. Frame numbers indicate time sequence.

TABLE 1 CHARACTERISTIC FEATURES BELONGING TO THE

Function of behavioural elements	Particulate intake	Gulping	Selection	
			Rinsing	Repositioning Back-washing
Movement pattern	-mouth opens by lower jaw and early protrusion -orobuccal and opercular cavities expand -opercular valves open late -skull is lifted -lower jaw closes protruded mouth and initiates compression	-mouth opens without protrusion -oral depression mainly -opercular valves open early in abduction -late protrusion closes depressed lower jaw	-mouth opens without protrusion -orobuccal and subsequently opercular expansion	-orobuccal depression -protrusion keeps the mouth closed -late opercular adduction -compression orobuccal cavity
Effects	-fast suction flow directed to the particle -food trapped into the pharyngeal slit	-bite of suspension enters the mouth slowly, suction even from the jaw angles -maximal suspension enclosed prior to oral compression	-pumping of water along the fixed particle -washing waste through the opercular slits	-inflow of water through the branchial slits a)merely repositioning the particle b)washing particles back into the orobuccal cav. -expulsion of waste through opercular slits -local retention of food in the pharyngeal slit
Reference EMG	-long LOP burst -low PCE and LAB V activity	-long LOP burst -low PCE and LAB V activity	long LOP burst	-short LOP burst
Anterior palatal organ	-narrows the pharyngeal lumen	-narrows the pharyngeal lumen	-fixes the particle	-manipulates and retains food particles locally
Posterior palatal and postlingual organ	-close off posterior pharynx and esophagus	-close off posterior pharynx and esophagus	-	-

DISTINCT BEHAVIOURAL ELEMENTS IN FOOD HANDLING

Spitting	Transport	Loading	Mastication	Deglutition
-orobuccal expansion few protrusion -mouth opens hardly protrusion -opercular and buccal compression	-posterior pharynx gradually expands	-posterior pharynx spaciously expands	-overall expansion of oropharyngeal and opercular cavities -elevation of the skull -retraction pectoral girdle -mouth widely open without protrusion in part. feeding -mouth closed by protrusion in suspensionfeeding	-compression of the posterior pharynx -small movement resembling mastication
-particles sucked into the orobuccal cavity and rapidly spat through the mouth	-food is propelled to the chewing cavity	-food is loaded into the chewing cavity	-the fixed food is crushed and ground -particles are prevented from escape to the anterior pharynx -anteriorly stored suspensions are prevented from escape through the mouth	-ground food is directed into the esophagus
-high LOP activity	-increasing PCE activity	-high PCE activity	-high LAB V activity -high PCE activity -high LOP activity open mouth: long closed mouth: short	-low LAB V activity
-	-		-	-
-occasionally active	-peristaltic waves propell the food caudally	-manoeuvre food between teeth and chewing pad	-fix the particle to be masticated -close off the entrance of the chewing cavity	-close off the entrance of the chewing cavity

Two other movement patterns in food handling.

Besides the particular sequence of movement patterns in Figure 2 gulping and spitting are regular components of feeding.

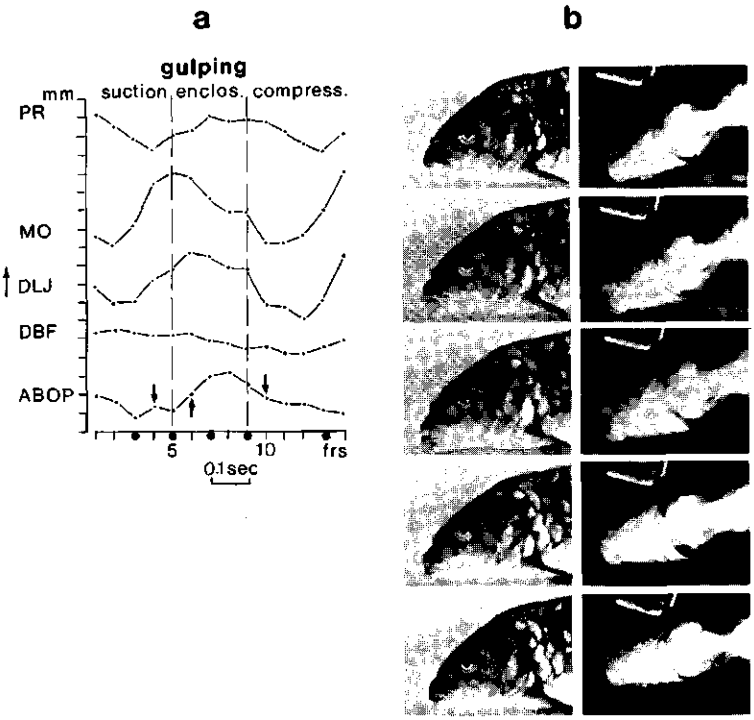


PLATE VII. Gulping a cladoceran suspension. (a) Movement graphs. (b) External views (24 frs./sec.). The approximate timing of the frames has been indicated (●) at the frame-scale in the graphs.
Suction is caused by oral depression mainly (frs. 2-5). Buccal and opercular expansion play a minor role. Protrusion only aids in mouth closure enclosing the bite of suspension (frs. 5-9) before lifting of the lower jaw causes oral compression (frs. 9-12). Opercular abduction occurs only at mouth closure (frs. 5-8) and for the most of it with open slits (↑). Abbreviations as in Plate II.

Gulping (Plate VII)

Carps fed on zooplankton (e.g. *Daphnia magna* of varied size) show a **'gulping'** mode of feeding (cf. Janssen, 1976). In the carp it is characterized by

a) aiming of the fish at high density spots in the cloud of zooplankton and

b) repetitive low intensity suction acts over long periods.

Contrary to particulate intake (Plate II), depression of the buccal floor is hardly involved (Plate VII; trace 4). Opercular abduction only occurs at mouth closure and for the most of it with open opercular slits (frs. 5-8).Therefore suction is mainly caused by oral expansion, abduction of the cheeks and opercula play a minor role. Protrusion only starts when the mouth is widely opened and aids in mouth closure even before the lower jaw is lifted (frs. 5-9). The upper jaws form a rostral hood over the enclosed suspension. The volume of the gulp is thus maximized by preventing its forward expulsion through the early lifting of the lower jaw. Ballintijn et al. (1972) demonstrated the different roles of the adductor mandibulae parts in such jaw movements. In gulping bites of water with suspended food particles are taken whereas at particulate feeding one specific particle is chosen. Filter feeding, the swimming around with the mouth kept fully agape over long periods, has never been observed in carps of yearclass I-III under laboratory conditions.

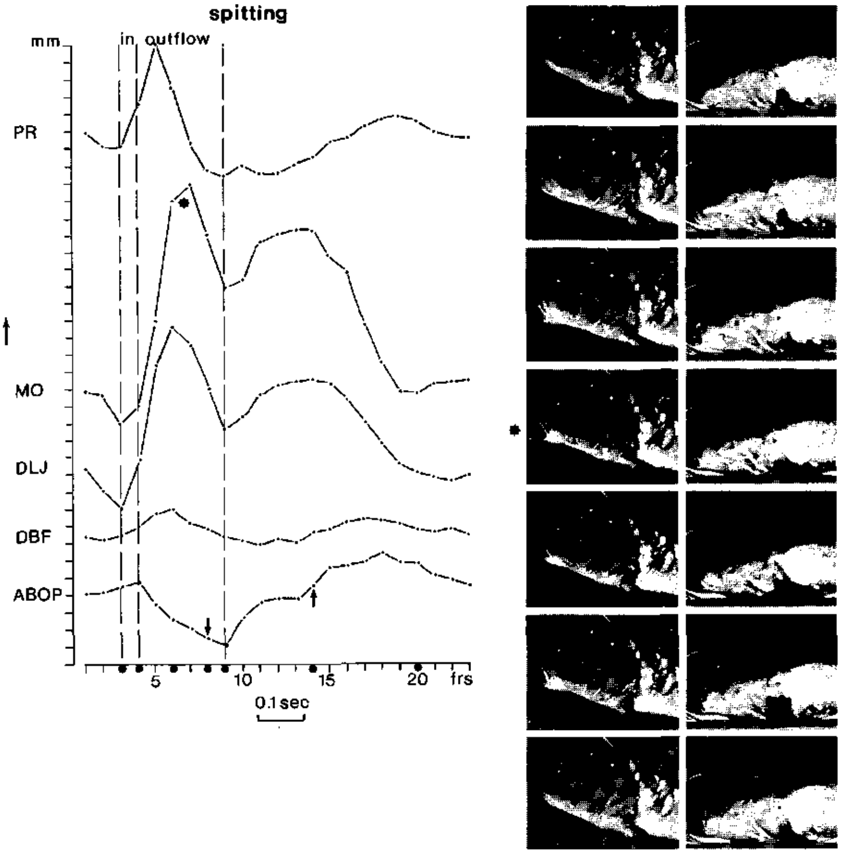


PLATE VIII. Spitting. (a) Movement graphs. (b) Successive views on the carp during an other spitting (24 frs./sec.). The approximate timing of the frames has been indicated (•) at the frame-scale in the graphs.
Following full orobuccal compression with widely open opercular valves (frs. 1-3) and subsequent inflow of water by closed protrusion (frs. 3-4), the mouth is rapidly opened and the unwanted particle expelled (*) by strong compression of the opercular and orobuccal cavities (frs. 4-9). Note the re-expansion with closed opercular valves (↓) once compression is halfway (frs. 9-14), possibly reversing the flow into rostro-caudad direction. Abbreviations as in Plate II.

Spitting (Plate VIII)

Spitting starts by closed expansion of the fully compressed orobuccal cavity, through lowering and protrusion of the jaws (Plate VIII, frs. 3-4). This rostral expansion effects inflow of water through the widely open opercular slits. As soon as the opercula adduct the mouth opens (fr. 4) and fast compression of opercular, and subsequently the orobranchial chambers effects a pressure wave expelling water and particles through the widely opened mouth (asterisk). Following spitting, compression is often interrupted by a second expansion. In this way the fish may reverse the direction of flow to the usual rostro-caudad pattern. Spitting movements of lower intensity with half open mouth occur and specific parts of the adductor mandibulae muscle (A 1α) may even direct the mouth opening ventrad by protrusion (Ballintijn et al., 1972).

The role of the palatal and postlingual organ in food handling

The above elements of feeding can not fully explain the total path of particle movement, neither the refined selection between food and non-food as apparent from gut contents (Wunder, 1936; Uribe-Zamora, 1975). Whereas anteriorly the transport is effected by a flow of water, manipulated by the varied movement patterns of the head parts, such volume changes play a minor role in posterior transport (Fig. 2).

The contributions of the muscular palatal and postlingual organs in feeding have been investigated by recording their local activities at six distant spots (Figs. 3,4). Note from these figures that the activity in these complex organs, without conspicuous subdivisions in their gross morphology, can be very local. This emphasizes their role in the precise proces of rejection and retention of particles. Their abundant supply with taste buds (up to $820/mm^2$), mucus and peculiarly arranged muscle fibers is discussed elsewhere (Sibbing et al., 1984). Local bulging of the palatal and postlingual organ was readily observed at mechanical or electrical stimulation, and has been used for localizing the electrode-tips during anaesthesia. In a freshy killed carp stimulation may even elicit a peristaltic wave travelling posteriorly. Similar observations have been reported by Berghe (1929) and Jara (1957).

To determine the role of the palatal and postlingual organ during all separate movement patterns of food handling each pattern must be recognized from the multichannel EMG records. For this aim the simultaneous activities in the LAB V, LOP and PCE reference muscles have been recorded (Figs. 3,4). Also light-cinematography served this goal. The movement patterns and their characteristic reference EMG have been summarized in Table 1.

Large food pellets allow a clear distinction of the subsequent feeding actions in the palatal and postlingual organs (Fig. 3a). Food-soil mixtures, which closely resemble the natural feeding conditions, evoke a high and widely differentiated activity pattern (Fig. 4b).

Intake

The activity in the palatal and postlingual organs at intake (Fig. 3a) may close off the narrow entrance to the posterior pharynx and prevents that the high suction force is also applied to the contents of chewing cavity and esophagus. They thus aid in directing the suction flow.

Selection

Once the pellet has been trapped in the narrow pharyngeal lumen, activity in the rostral and lateral parts of the palatal organ (traces 1-4) indicates gustation and internal selection. Synchronous bursts in the levator operculi muscle indicate lower jaw depression. Long LOP bursts point to rinsing whereas short LOP bursts characteristically belong to closed protrusion movements (cf. Fig. 2). As the internal effects of closed protrusion on the food are invisible it is only indicated by the general term positioning. Likewise has been done for the other EMG records (Figs. 3,4). The activity of the palatal organ may also serve for a repeated test of the palatability of the particle.

Transport and loading

Progression of activity from the anterior to the posterior parts of the palatal and postlingual organ (traces 4-6) corresponds to propulsion of the pellet to the chewing cavity in the X-ray movies. Most often propulsive waves rapidly succeed (Fig. 3a, arrows). They become gradually accompanied by activity in the PCE muscle (lower trace) initiating expansion of the chewing cavity.

Note that the postero-lateral part of the palatal organ (Fig. 3a, trace 4) acts in selection as well as in transport and mastication, indicating its boundary-position between the functionally distinct antero-lateral and posterior areas.

The end of anterior palatal activity announces loading of the pellet on the pharyngeal teeth (Fig. 3a, ld.). The PCE muscles spaceously expand the chewing cavity while the posterior parts of the palatal and postlingual organs continue their propulsion of food on to the now depressed teeth.

Mastication and deglutition

The posterior parts of the palatal and postlingual organs are highly active, fixing the pellet to be masticated (cf. Plate Vb) during the successive power strokes. They will also obstruct the escape of ground food back to the anterior pharynx. Similar activity is observed at deglutition (Fig. 3a, dgl.) whereby the constrictor pharyngis muscle aids in compressing the chewing cavity (Sibbing, 1982). Their combined actions direct and propel the ground food into the esophagus. Activity in the expansion muscles of the chewing cavity (PCE) is now conspicuously lacking.

Reloading

Prior to mastication of a second bite, the pellet is repositioned by palatal-postlingual activity and closed protrusion (short LOP bursts) (Fig. 3a, reloading). When food particles are washed back into the orobranchial cavity, as often seen in the X-ray movies (cf. Plate IIId), further mastication requires transport and loading. The reloading pattern then even more resembles the events after intake.

The palatal and postlingual organs display an apparent regional differentiation in functioning. The anterior and lateral parts are active in trapping, gustation, selection and positioning, whereas the central and posterior parts are involved in transport, loading, mastication and deglutition. Contrary to Jara's hypothesis (1957) the palatal or postlingual activity was never measured during respiration, even if it was forced to be intensive.

Adjustment of the feeding sequences to the type of food

To determine the adjustments of the movement patterns and the palatal-postlingual activities to the type of food, different types have been fed.

Movie and EMG-records showed conspicuous differences in the presence and repetition of the distinct food handling patterns. The feeding sequences are analyzed below and characterized in Table 2. Only the major differences with the discussed pellet sequence are reported. They occur mainly in intake, selection and mastication.

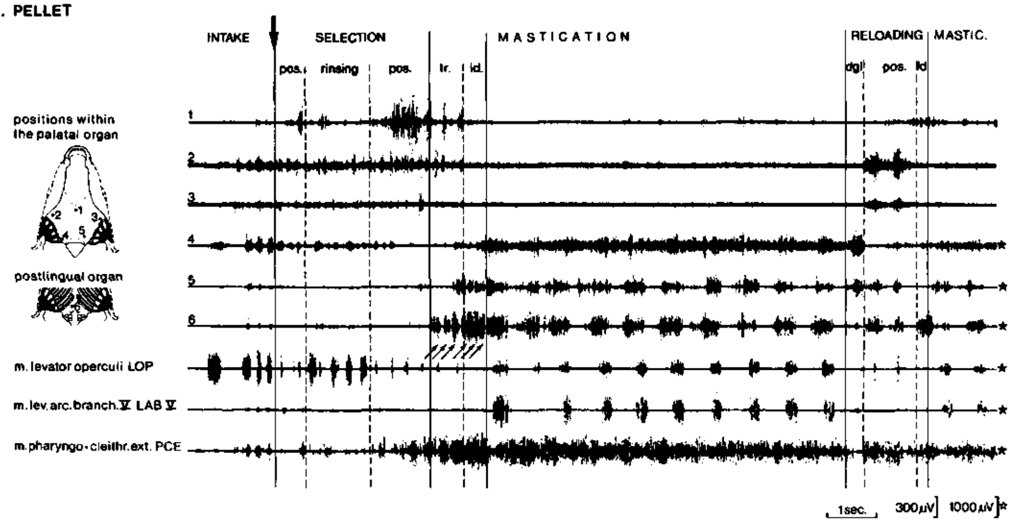
Barley

Grains of barley generally demand frequent repositioning to manoeuvre the small dense particle from the branchial to the medial area, providing an appropriate grip for transport. Back-washing movements prevent loss of the heavy particle through its sinking from the lateral depressions in the buccal cavity into the large first branchial slits. Rinsing is never observed. Mastication may last for several minutes and requires crushing prior to grinding (cf. Sibbing, 1982, fig. 15).

Earthworm (Fig. 3b)

The earthworm-sequence shows that the palatal activity locally changes (Fig. 3b; arrows) and is even maintained in the anterior parts during mastication. This

a. **PELLET**



b. **EARTHWORM**

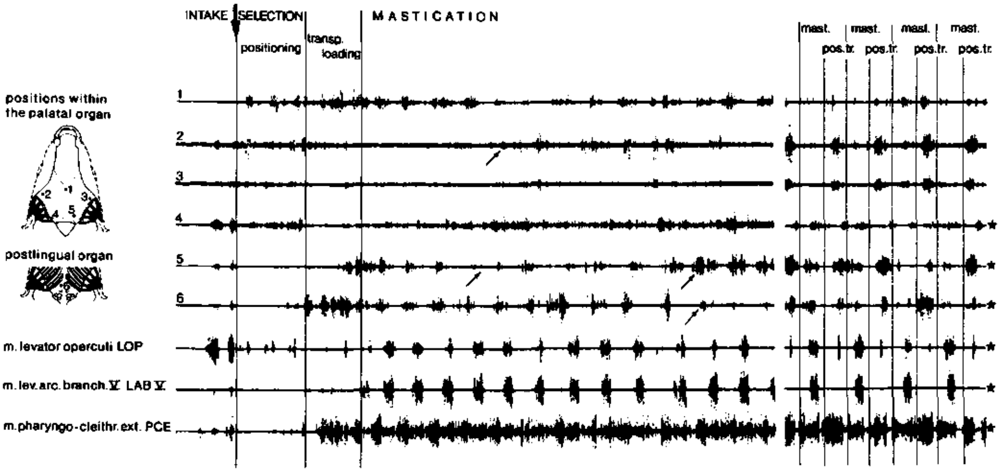


FIG. 3a. Palatal and postlingual activity during pellet feeding. Activity pattern of the muscular palatal and postlingual organs at six indicated places during eventually succesful intake (large arrow) and internal processing of a pellet. The three muscles below monitor jaw movements (LOP) and mastication (LAB V, PCE).

The anterior half of the palatal organ (traces 1-3) is active during intake and selection and involved in gustation, rinsing and positioning (pos). Then the activity passes away from the anterior to the posterior parts of these organs (traces 4-6) which serve transport (tr), loading (ld), mastication and deglutition (dgl). The postero-lateral area (trace 4) overlaps most of these actions. The repetitive arrows mark the peristaltic waves in transport. The patterns are discussed in the text.

FIG. 3b. Activity pattern in earthworm feeding (same experiment). Note the overall similarity in the pattern, compared to Fig. 3a. Activity in the anterior palatal organ (traces 1-3) is however maintained during mastication. Palatal and postlingual activity vary locally (arrows), reflecting the local manipulation of the sprawling worm during mastication. In a later stage of processing masticatory cycles (LAB V activity) alternate with positioning-transport actions (short LOP bursts and overall palatal activity) suggesting an intermittant transport of the masticated worm through the chewing cavity.

reflects more the length of the sprawling worm, being masticated at one end and immobilized by the palatal organ at the other, than an essentially different type of processing. Due to the length of the worm feeding actions overlap. No rinsing occurs. Closed protrusions aid in positioning to improve the grip on the long prey. Transport of the worm through the chewing cavity may alternate with mastication (Fig. 3b). Such an intermittant transport was actually seen in an X-ray scene, after the worm had been injected with barium sulphate in its coelomic compartments. Mastication proceeds merely by grinding (Sibbing, 1982; Fig. 15).

A soft lump of tubificids was taken by forceful suction. The carp apparently could not achieve a proper grip on the lenient mass and tried to disperse it in smaller clusters. This is concluded from the abundant repetition of closed protrusion movements, positioning the food and washing it through the orobranchial cavity. Even spitting and re-intake are applied for renewing the grip. During grinding protrusion of the upper jaws kept the mouth closed, preventing tubificids from being expelled through the mouth.

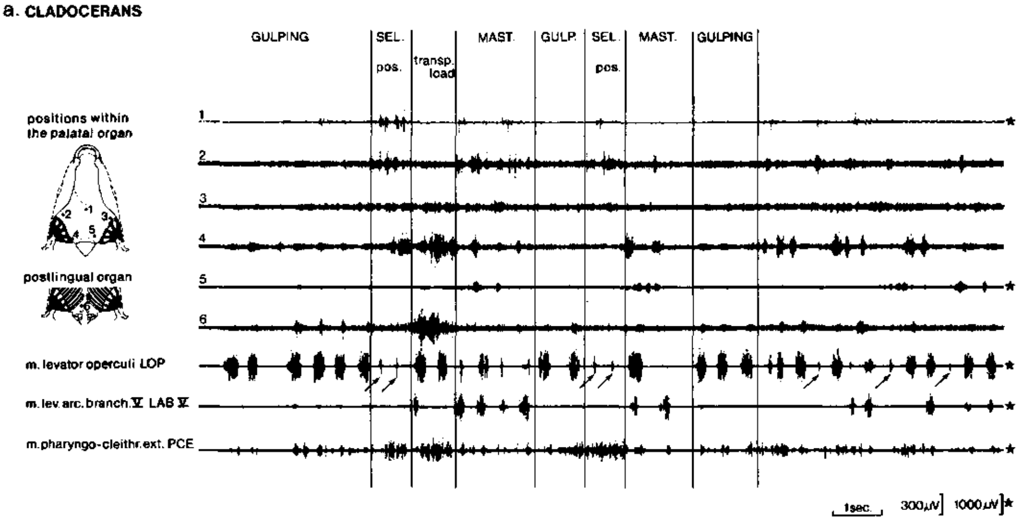
Zooplankton (Fig. 4a)

Whereas the above larger food items elicited 'particulate feeding' sequences, cladocerans were taken by repetitive 'gulping' (cf. Plate VII; Fig. 4a, long LOP bursts without high LAB V activity). While suspending ground pellets into the tank an eager carp attained frequencies of even eight gulps within a second. This accumulates particles from small volumes of suspension into the pharynx. Selection typically proceeds by palatal activity and closed protrusion (short LOP burst without LAB V activity). This movement will however also serve to wash particles from all over the branchial sieve back to the medial area between palatal and postlingual organ. In this way closed protrusion serves **recollection** of the filtrate for transport. Also here protrusion of the upper jaws generally keeps the mouth closed during mastication, preventing the escape of free floating particles through the mouth. Thus the external profile of the masticating fish will markedly differ at particulate feeding and gulping. The separate gulping sequences are of short duration.

Tubifex-soil mixtures (Fig. 4b)

Substrate feeding was analyzed by offering a peaty pond soil intermingled with tubificids. Gulping as well as particulate intake was observed.

Feeding on food-soil mixtures asks increased activity in the palatal organ (Fig. 4b, traces 1-3) overlapping most other feeding actions. Closed protrusions (short LOP bursts) in combination with anterior palatal activity are conspicuously frequent



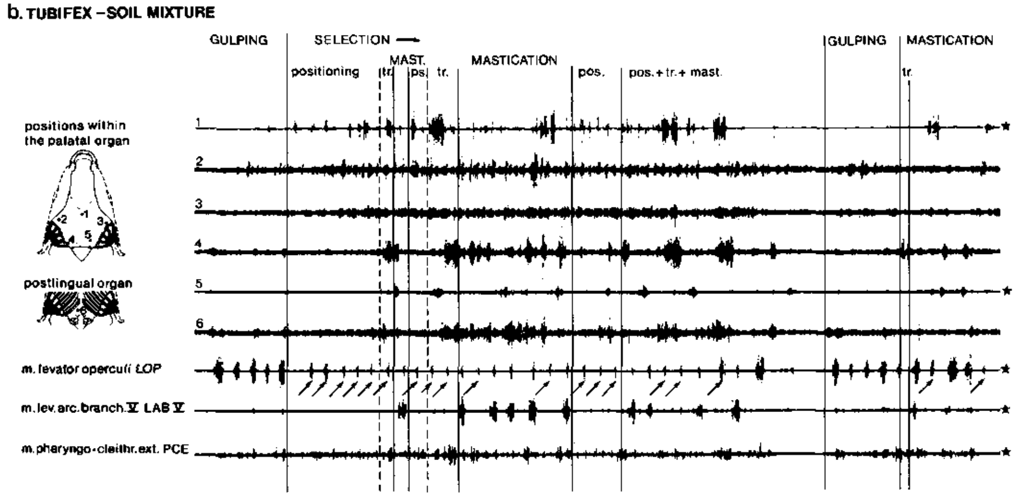


FIG. 4a. Activity pattern in zooplankton feeding (cf Fig. 3a). Intake of the cladoceran suspension proceeds by repetitive gulping (merely long LOP bursts). Subsequent anterior palatal activity (traces 1-3) and closed protrusions (arrow) will wash the cladocerans back from the branchial sieve recollecting them for transport (traces 4-6) and mastication (LAB V activity). Such short sequences are repeated over long periods. Further discussion in text.

FIG. 4b. Substrate feeding. Activity pattern during processing of a peaty pond soil containing tubificids (same experiment as Fig. 4a). The anterior palatal organ (traces 1-3) has a prominent role in selection between food and non-food particles, frequently accompanied by closed protrusion (arrows).
Selection overlaps mastication (LAB V) and transport and takes much handling time. Further discussion in text.

in selection (Fig. 4b; arrows), gradually purifying the mixture (see discussion) and recollecting small food particles from the branchial sieve. Note that processing of such mixtures requires a considerable handling-time (cf. Fig. 4b). Spitting is generally employed for coarse selection, allowing choice at re-intake, often by gulping the suspended particles. A similar behaviour is observed at searching when the carp keeps sampling the substrate by a short sequence of intake, gustation and spitting i.e. **probing.**

FOOD	UNITS OF BEHAVIOUR							
pellets	P	RI	RP-BW	T	L	C	$\boxed{\text{GR}}$	D
barley	P		$\boxed{\text{RP-BW}}$	T	L	$\boxed{\text{C}}$	$\boxed{\text{GR}}$	D
earthworm	P		RP-BW	T	L		$\boxed{\text{GR}}$	D
lump of tubificids	P		$\boxed{\text{RP-BW}}$-RC	T	L		$\boxed{\text{GR}}$	D
cladoceran suspension		$\boxed{\text{G}}$	BW-RC	T	L	C	GR	D
tubifex-soil mixture	P or G		$\boxed{\text{BW}}$-RC	T	L	C	GR	D

TABLE 2. Composition of feeding sequences according to the type of food. Conspicuously repeated patterns are indicated by a square. Probing and spitting do not lead to food consumption and are considered separately from the feeding sequence (see text).

P	particulate intake	RP	repositioning	T	transport	GR	grinding
G	gulping	BW	back-washing	L	loading	D	deglutition
RI	rinsing	RC	recollection	C	crushing		

FOOD HANDLING MECHANISMS AND THEIR LIMITATIONS

Postcapture feeding behaviour, divided into buccal manipulation, pharyngeal manipulation and pharyngeal transport in generalized euteleosts (Lauder, 1983) is at least in cyprinids split into a chain of distinct functional patterns, wherin the buccal, pharyngeal and opercular mechanisms closely interact. (Table 1). The timing and sequence of protrusion, orobuccal and opercular expansion and the moment of opening of the mouth and opercular-branchiostegal valves allows a high plasticity in movements.

From its feeding ecology and diet the adult carp appears to be an omnivorous fish, feeding at different levels of the watercolumn and the food chain, whenever and wherever food is available (Uribe-Zamora, 1975; in Sibbing, 1982). In Table 4 a list of generally available food types is given. From these bottom invertebrates (chironomids and other dipteran larvae, tubificids, copepods), zooplankton (preferably large cladocerans and copepods) and soft littoral vegetation (*Lemna minor, Glyceria fluitans*), but especially its fauna (gasteropods, oligochaets, trichopter larvae, copepods), according to season and availability, are exploited. Even aerial insects are engulfed from the watersurface.

The omnivorous feeding habits of the carp raise the following questions. Does the feeding efficiency, taken as time expenditure to obtain and handle a food type, or taken as the energy costs-gain ratio in feeding, widely differ for different types of food? Do specializations for one type necessarily lower the feeding efficiency for others?

These questions demand a quantitative approach and much more knowledge than now is available. However the present qualitative data about the type and sequence of movement patterns employed in food processing allow an analysis of their effect on the food. Which optimizations in structural tools and their application characterize the separate feeding elements and which restrictions follow for others? In such a way the relations between structure-function components and their impact on the available food and ecology of a fish type can be deduced. Comparisons between closely allied species may then provide insight in the extent of their niches. As the efficiency and limitations of feeding is bound to its component parts the distinct feeding elements are discussed, starting at the search for food.

Search and detection of food, a survey

Carps in search for food are typical stayers (Boddeke, Slijper et al., 1959) feeding continuously on pelagic or benthic organisms, repetitively probing and scanning the substrate. Wunder (1927) investigated a variety of teleosts, including the carp, to determine which of the diversified sense organs are involved in food detection. Jönsson (1967) elaborated Wunders experiments on one year old carps and included an analysis of their daily rhythm. Carps have a high endogenous activity level at dusk and night. They are, however, readily trained to feed at any time of the day. Other major conclusions from this author are incorporated below.

Abiotic conditions such as light and turbidity of the water as well as the stimuli produced by the food determine which sense organs are involved in detection.

At pelagic feeding the carp reacts on and is guided to its food by vision. Size, shape, contrast, colour and motion of the prey will further differentiate visual discrimination and the reactive distance. A light intensity of 10^{-1} mc (metercandle), corresponding to late dusk, marks the lower threshold for effective visual location of food by most fishes (Blaxter, 1970), with some notable exceptions. The lateral line organ senses actively moving preys in laboratory tanks but its capacity to discriminate prey over long distances from other moving stimuli, as in a natural situation, is doubtful. In the pike the lateral line is effective in detecting water turbulence at distances less than 10 cm (Wunder, 1936). When vision is poor or the food inactive smell guides the carp by trial and error to the food. Olfactory organs generally have a high sensitivity and are long-range chemoreceptors. In fish they are reported to be more often associated with social contacts than with feeding (Hara, 1971). When carps feed on cereals or other encapsulated seeds, often offered in fish farms, smell stimuli will be low.

At bottom feeding taste is the main detector in search for food. The fish is alert on prey even at some distance from the mouth as taste buds are exposed on barbels and fins, and are spread even over the head and general body surface (Herrick, 1904). Contrary to reports of Jönsson (1967) the expected role of touch in detecting of food has not been demonstrated in the carp , neither by experimental nor by structural data.

Within the oropharyngeal cavity taste buds further serve control and selection of particles to be swallowed (cf. Sibbing et al., 1984). The decision for processing requires this internal evaluation. To distinguish between the external and internal moments of choice the terms 'choice' and 'selection' are respectively used.

The probing mode of searching and the abundant supply of external and internal taste buds allows intensive substrate feeding. This extends the exploitation of the available area with its depth. Experiments from Suietov (1939) show carps to penetrate more than 12 cm into a silty bottom. No general ecological areas (bottom, open water, surface, littoral) seem to be excluded from exploitation by the carp due to its searching behaviour, except the open water at dark.
The sensory abilities seem hardly to exclude major categories of food from detection by the carp (cf. Table 4). Detailed knowledge of discrimination by the individual senses of the carp is scarce in literature.

Food intake behaviour

The dominant mode of prey capture in teleosts consists of a combination of suction (by rapid expansion and compression of orobuccal and opercular cavities) and forward motion (by forward suction of the fish itself, protrusion and swimming) (Muller and Osse, 1984). They distinguish a series of feeding types, based on the relative contributions of these components with the moment of opercular valve opening as an important characteristic. Optimizations of prey capture techniques are discussed by van Leeuwen and Muller (1984), focussing on predator-prey distance and prey velocities. These studies provide a frame for analysis of food intake in the carp.

In the carp swimming hardly contributes to food intake.This is readily observed from its deep body shape and the slow approach to the food. At bottom feeding the substrate even prohibits overswimming the food. Swimming is not an essential component in feeding on stationary preys. Drenner et al. (1978) has however demonstrated that copepods are far more able in escaping predation than cladocerans.

Grasping large particles with the lips was occasionally observed and served to remove gravel from underlying tubificids. It may well be applied in a natural situation e.g. for taking snails from macrophytes. No biting occurs in the carp, as the only teeth of cyprinids lie posteriorly in the pharynx.

Two distinct patterns of food intake are evident in the carp. Their mechanisms and effects are compared in Table 3.

Particulate intake (Fig. 5)

During expansion of the slow swimming fish the late opening of the opercular and branchiostegal valves will prevent inflow through these valves and thus increase the water velocity in the mouth. Expansion is however slow (ca. 160 msec.) compared to predacious fish as a pike (ca. 40 msec., van Leeuwen and Muller, 1984). Water velocity in the mouth opening is further increased by protrusion of the upper jaw creating a small rounded aperture of the mouth. Besides protrusion brings the mouth closer to the food without cost for adding impuls to the water or the fish and thereby causes a directed flow with respect to the mouth aperture. Combination of these characters results in a fast and directed suction flow applied close to the particle. Such flow velocities allow intake of particles with higher densities than the water and increase the distance from which can be sucked. Forward suction of the fish may well contribute to penetration into the bottom substrate.
Sustained opercular abduction and the impuls of the water maintain the flow caudad during oral compression. The particle will be trapped in the narrow slit between pharyngeal roof and floor whereas the water is expelled through the branchial and opercular slits. It is supposed that the main flow passes through the first branchial slit, serving as a shunt (hyoid-shunt cf. van Leeuwen, 1984). The gill filaments may be adducted to reduce the gill resistance in the suction flow, as during strong ventilation (Ballintijn et al., 1972).

Protrusion also permits the carp to apply its mouth ventrad and closely to the bottom without need for vertical position of the body axis at intake. In the spindle-shaped gudgeon this will serve to maintain its position in fast flowing streams (Alexander, 1970). In the deep bodied carp, living in stagnant waters, it allows a continuous probing of the bottom by slow swimming. Besides it permits a rapid escape from a predator during bottom feeding. Protrusion is thus highly functional. The mechanism of protrusion in the carp was investigated by Ballintijn et al. (1972). Different parts of the adductor mandibulae muscle effect forward

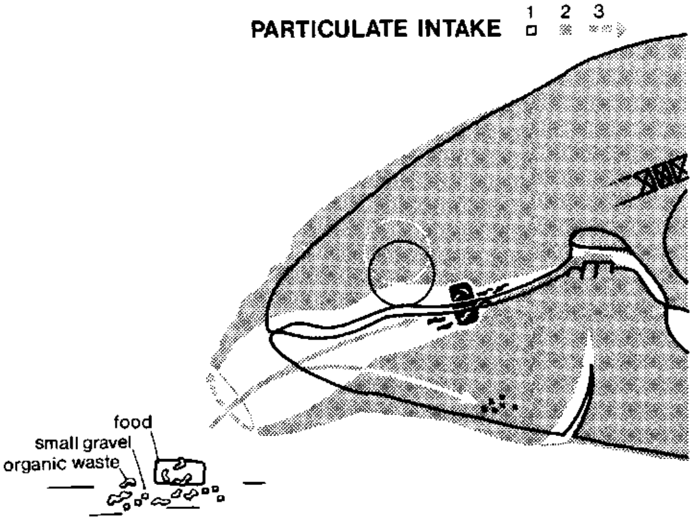


FIG. 5. Particulate feeding, intake. Following full compression (line image), overall expansion of the head and protrusion (dark image) cause a fast flow and directed suction in the small opening of the mouth, aimed to the particle. During suction the posterior chewing cavity is closed off by the muscular palatal and postlingual organs. Food and light organic waste are trapped in the narrow pharyngeal cavity whereas heavy particles sink into the first branchial slit. The protruded mouth is closed by the lower jaw. Sequence of images at the top. Further explanation in Table 3 and text.

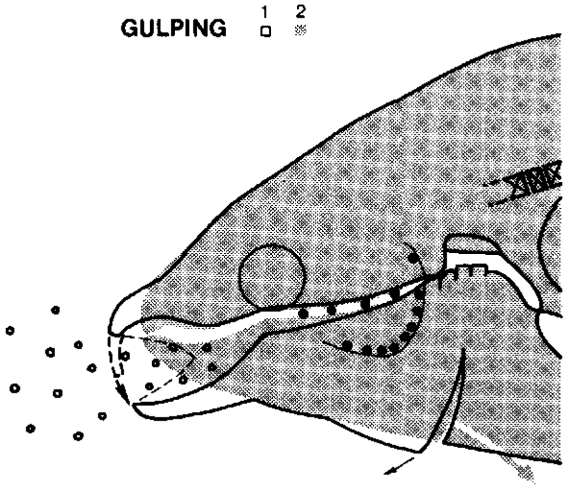


FIG. 6. Gulping proceeds by oral depression mainly (line image). It causes a slow flow of small volumes from all directions into the wide slit-shaped mouth. Late protrusion encloses the maximal volume taken. Opercular abduction only occurs as the mouth closes. Buccal compression (dark image) passes particles through a narrow pharyngeal slit to the branchial sieve. Recollection for transport proceeds later. Repetitive gulping accumulates particles and is employed for intake of suspensions over long periods. Sequence of images at the top. Further explanation in Table 3 and text.

PARTICULATE INTAKE	GULPING
- protrusion renders mouth cavity tube-like, directing the flow to a particular particle	- mouth cavity with open jaw angles; causing inflow from all directions
- protrusion allows ventrad aiming of the mouth to the particle	- mouth opening generally terminal; initially hardly protrusion
- fast and voluminous flow by protrusion and extensive depression of oral and buccal floor; closed opercular abduction important	- slow flow of small volumes by depression oral floor; buccal and opercular expansion play a minor role; valves open early
- particle sucked into the anterior pharynx	- particles sucked into the oral cavity
- mouth closure by lifting the lower jaw, compressing the open oral cavity	- mouth closure by late protrusion; oral cavity not compressed
- water expelled caudally; particle retained in the central pharynx	- maximal volume of water with particles is enclosed by a rostral hood and pressed slowly to the branchial sieve by oral compression
- single actions at high energy-costs	- repeated low energy-costs actions over long periods
- suited for suction of dense or less accessible particles	- suited for gulping of suspensions

TABLE 3. Intake patterns and their effect on the food, explaining the differences between particulate intake and gulping.

protrusion ($A_{1\beta}$), downward protrusion ($A_{1\alpha}$) and lifting of the lower jaw (A_3 and A_2). The variable coordination of their actions allows a versatile aiming of protrusion to the food. The mechanics of head expansion for creating a suction flow has been studied firstly by Liem (1967) using cinematography and Osse (1969) adding electromyography. Such studies are still lacking for the carp. The mechanical couplings in its head have however been studied (Ballintijn, 1969).

Gulping (Fig. 6)

Low intensity suction and the early opening of the opercular valves reduce volume as well as velocity of the water and suspended particles at each gulp and lowers its energy costs. The initial absence of protrusion causes a less directed flow even from the jaw angles. As suspended particles are of about the same density

as the water, have a limited movement and are widely dispersed neither high velocity nor directed flow are demanded. Therefore gulping is appropriate to take suspensions over long periods. Small volumes at each gulp may be demanded for filtering the suspension effectively over the branchial sieve maintaining limited and about equal branchial slits. Food-soil mixtures and particulate intake probably require a large first branchial slit for shunting large volumes of water and debris. Movement analysis of the branchial arches could falsify such hypotheses.
Late but extensive protrusion encloses the ingested suspension by forming a characteristic rostral hood prior to oral compression. The maximal retainable suspension is pressed caudad through the narrow buccopharyngeal slit, which improves particle-wall contact for gustation and enhances the even spreading of the suspension over the branchial sieve.

Limitations (cf. Table 4). Size, density, velocity, distance and location of the food in the habitat impose different demands to the fish and are directive characters in the optimization of food capture techniques.

Large preys are excluded from intake by a carp (SL 22 cm) due to its short jaws and the small gape of the mouth at protrusion. The maximal diameter of the protruded circular mouth is about 9% of the standard body length (SL) for carps ranging between 10-25 cm SL. The values for larger carps decrease to about 7% SL. The fish is also unable to take bites from larger food objects like fish and macrophytes as oral teeth are absent. This also facilitates the escape of struggling prey.

Fast preys easily escape. The deep body shape as well as the predominance of red muscle fibers in the trunk (Boddeke, Slijper and Van der Stelt, 1959) and headmuscles (Akster, 1981; Akster and Sibbing, 1982), allowing prolonged activity but contracting slowly, render the carp a slow swimming and slow feeding stayer. Though its maximal burst speed is around ten body lengths per second (Blaxter, 1969), no reports of such velocities in feeding have been found. The endurance or cruising speed of the carp is around 1.5 body lengths per second. These features exclude hunting after fast preys, even in open water. The small aperture of the mouth makes filter-feeding by overswimming the water inefficient.

Foods of high density, such as some plantseeds, lie within reach for intake due to the large velocity of flow. Particles of low density may be taken from more distant, less accessible locations like crevices due to the highly directed and fast suction flow during protrusion.

Selection (Figs. 7,8)

Size selection between particles should be distinguished from selection between food and non-food, as they are achieved by different mechanisms.
The minimal mesh-width of the carps branchial sieve lies between 400-500 µm, minimized to 250 µm if only smaller plankton is abundant (Uribe-Zamora, 1975). Only the width of the plankton determines its retention, thus irrespective of its length. The actual mechanism of the branchial sieve is not known which limits the insight in selective predation on zooplankton (cf. Wright et al., 1983). It is important for many other planktivorous fish species (e.g. silvercarp, big head, herring, menhaden).
At bottom and substrate feeding, mixtures of food, anorganic sediment and organic debris impose high demands on the selection mechanism prior to further processing. Fine anorganic sediment (< 2 mm) contains mainly particles below 250 µm which are passively lost through the branchial sieve (Uribe-Zamora, 1975). Though she reports larger inorganic particles to be not ingested, due to their size and density (2.6), this is certainly not true at bottom feeding. Ingested heavy medium sized particles such as sand grains and small gravel will readily sink into the large first branchial slits by gravitational deposition (Fig. 5). Larger particles are expelled by spitting (see below). Active selection thus appears mainly to involve the separation of small to medium sized organic waste (250 µm - 9% SL) with densities comparable to water. Though the separation of food and non-food is not complete (Wunder, 1938; Uribe-Zamora, 1975) it is still highly effective. The latter author found only 3% of the fine sediment to be retained with the food.
How is active selection internally achieved? It is commonly accepted that selection between food and non-food proceeds within the buccopharynx. Abundant taste buds line this cavity (up to 820/mm^2 cf. Sibbing et al., 1984) and allow gustation as long as particles roll along its walls. Matthes (1963) supposes cyprinids to select by spitting, retaining food particles by entangling them in mucus. Spitting is however a coarse mode of selection. Robotham (1982) presumed also buccal mucus to effect selection at detritus intake of the spiny loach. More dense particles would escape mucous entrapment as they are given higher velocities (in our view impulse). Our results show that the palatal organ is hardly involved in spitting and that palatal activity as well as closed protrusion appear basic in separation and refined selection between organic waste and food. This has been overlooked completely.

According to the size of the soiled food and the amount of organic waste different mechanisms of separation and selection are employed by the carp. These are discussed below and illustrated in the Figures 5-9.

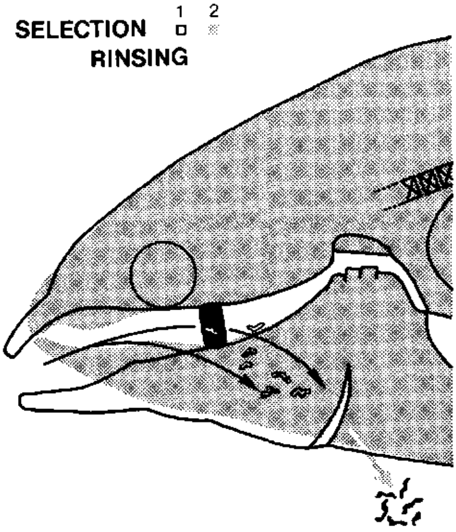


FIG. 7. Large immobile particles may be coarsely rinsed by repetitive and intensive pumping, washing away the waste and possibly fine food particles through the branchial slits. In the meantime the palatal organ clamps the large food to be retained. Sequence of images at the top.

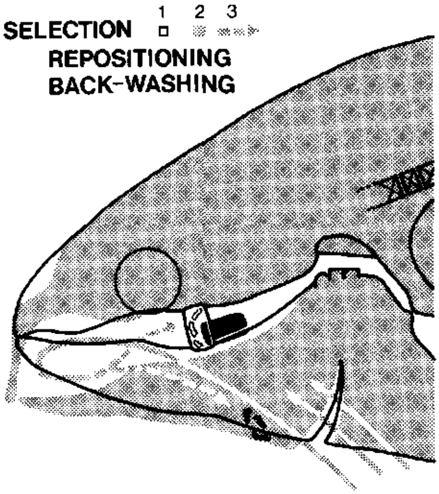


FIG. 8. Selection and graded purification of soiled items is achieved by repetitive repositioning and even backwashing movements. Particles are resuspended in the oral cavity by orobuccal expansion, aided by inflow of water (arrows) through the opercular valves. i.e. *closed protrusion*. Subsequently (pecked arrows) orobuccal compression will expell the waste through the branchial slits, whereas food will be retained by local and selective fixing between palatal organ and branchial floor. The ability for refined selection decreases with increasing food size. Closed protrusion is also employed for mere repositioning to improve the grip on the food and furthermore for recollecting food from the branchial sieve for transport. Sequence of images at the top.

Rinsing: cleaning a large immobile food particle from few waste (Fig. 7)

Large food, trapped in the anterior pharynx (cf. Plate IVa), is cleaned from waste particles by some regular strong pumping movements (cf. Fig. 2), flushing water along the fixed particle and simply expelling waste (and fine food particles) with the water through the branchial slits. Absence of such rinsing movements in the processing of small suspended food will be related to the large risk of loosing food in the flow of water. The same applies to handling larger actively moving preys (e.g. earthworm).

Repositioning and back-washing: refined selection between food and non-food (Fig. 8)

Closed protrusion (Plate III) has different effects, depending on the food. In mere repositioning it effects an improved grip for further transport (e.g. at large particles). Back-washing allows a sustained gustation by rolling the particles along the sensory orobranchial walls, possibly dissolving taste substances to reach the taste buds. During compression it serves to expel waste through the branchial slits.

In substrate feeding (Fig. 4b), back-washing effects a resuspending of food and non-food particles in the orobuccal cavity, improving their separation, aided by differences in specific gravity. Food is gradually purified, accompanied by expulsion of waste through the opercular slits. During expulsion of waste the gill filaments are supposed to be actively adducted for their own protection as well as to reduce the gill resistance in the flow of water. The large first branchial slit may well shunt the waste.

During repositioning and back-washing the antero-lateral part of the palatal organ, and the same probably holds for the muscular lining and gill rakers of the branchial arches, plays an active role in the compressive phase (cf. Figs. 3,4). Local bulging by muscular activity will clamp and retain food particles between roof and floor whereas waste is expelled with the flow of water. Frequency as well as amplitude of repositioning and back-washing are highly variable and most probably related to the actual location of the food and non-food. This mechanism largely explains the slit-like construction of the pharyngeal cavity with its small distance between roof and floor effecting close contact and effective selection. The morphological substrate for such a local and selective action, including the role of mucus, is discussed separately (Sibbing et al., 1984). The branchial surface appears to play an important active role in selection and purification as a counterpart of the palatal organ. This aspect should be distinguished from its function as just a branchial sieve. Closed protrusion is basic to repositioning and back-washing and this movement pattern appears of primary importance at internal manipulation and purification of food in cyprinids. It is of crucial importance in substrate feeders where internal gustation is not merely a final control but the decisive point of selection in food acquisition.

Spitting: ejection of any unwanted material (Fig. 9)

Spitting serves to expel unpalatable (e.g. watermites) or even harmful particles (note the vulnerable gill filaments), to expel heavily soiled mouthfulls, to disperse unmanageable large humps into clusters (e.g. a lump of tubificids) before re-intake and to expose hidden food during bottom inspection. Protrusion may direct the water jet in the latter process.

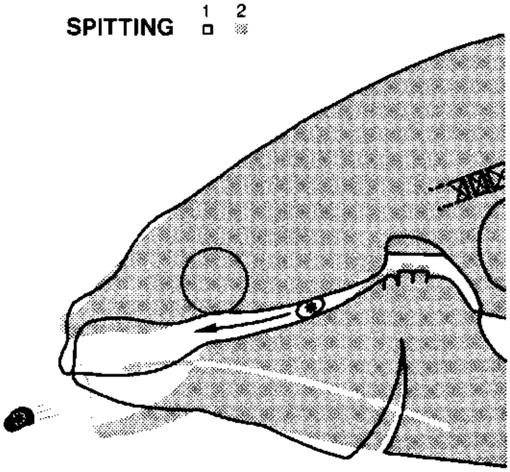


FIG. 9. Disliked particles, heavily soiled food and less manageable humps of food are rejected by spitting. An initial closed protrusion washes the particle back into the orobuccal cavity, sucking water from the open opercular cavity (open image). A pressure wave by sudden adduction of the opercular and buccal walls drives the particles rapidly through the widely opened mouth (dark image). Spitting may also serve exposure of food hidden in the substrate. Sequence of images at the top. Further explanation in text.

Spitting is a reversed suction pump action of the orobuccal and opercular cavities (cf. Plate VIII), initially sucking water and particles from the pharynx back to the oral cavity and then propelling it through the mouth by compression. The palatal and postlingual organs are occasionally active but, contrary to Matthes' opinion (1963), do not play an essential role in spitting. Spitting differs from coughing which occurs at the end of the compressive phase of a respiratory cycle and effects a reversed flow over the gills cleaning them from adhering particles deposited by the respiratory flow (Ballintijn, 1969; Osse, 1969). Coughing occurs at regular but long intervals and is not involved in feeding. It is frequently observed during stress of the fish e.g. after anaesthesia.

Limitations (cf. Table 4). The carp has highly developed structures and mechanisms for selection between food and non-food, allowing it even to exploit heavily soiled food areas. Refined selection requires the cooperation of roof and floor of the anterior pharynx. Large and flat objects (e.g. macrophytes and fish) impede such contact and are therefore not suited for such processing. Rinsing appears to represent a coarse alternative mode of selection. Limitations of food resources further focus on the inability to retain fine particles (< 250 µm). This should also exclude the smaller part of detritus, benthic diatoms and small plankton from the diet of the carp.

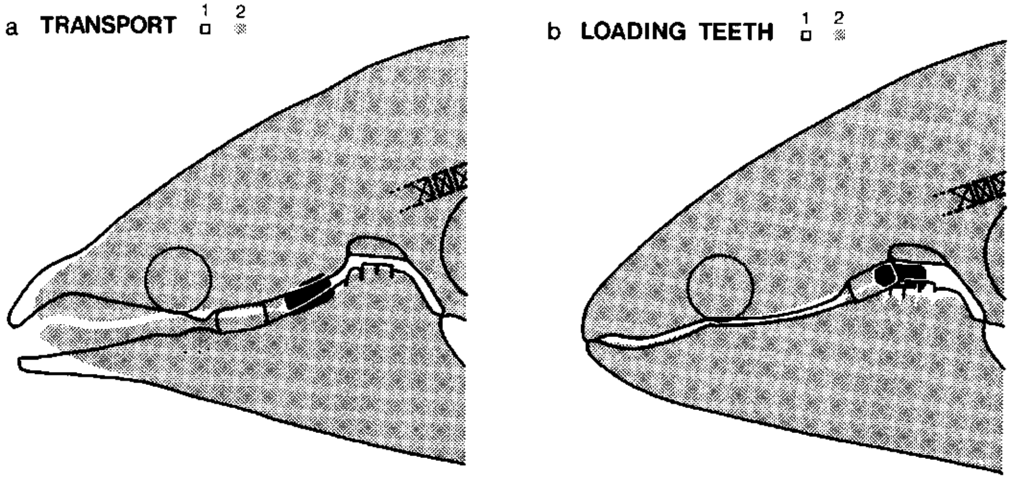


FIG. 10. (a) Transport of the purified food results from a peristaltic propulsive wave in the palatal and postlingual organs which cooperate like a piston. Whereas the anterior pharynx remains fully compressed, the pharyngeal teeth are slightly depressed allowing easier passage towards the chewing cavity. (b) Loading of the chewing cavity requires and additional large expansion of it to make way for the food. Sequence of images at the top.

Transport and loading (Fig.10)

These actions are hardly recognized from the exterior of the fish. Transport of the largely purified food towards the chewing cavity is effected by the posterior half of the palatal and postlingual organ (cf. Plate IVb; Fig. 3a). These opposed muscular pads cooperate like a piston and transport the food caudad by a repetitive peristaltic propulsive wave (Fig. 10a). Transport marks the transition of food movement by a flow of water into food movement by muscular peristalsis. Loading the chewing cavity with food (cf. Plate IVc) requires continued propulsion by the palatal and postlingual organ and extreme depression and abduction of the pharyngeal bones making way for the food (Fig. 10b).

How are small particles, trapped in the branchial sieve, manoeuvred into the esophagus? This appears one of the many unsolved problems in plankton straining. Our records of carps gulping cladocerans (Fig. 4a) show repetitive closed protrusion movements, accompanied by palatal activity, prior to further processing. As the suspensions offered where free from waste these movements will mainly serve for recollection of particles by washing them back from the branchial sieve. The palatal organ aids recollection by fixing them in the central pharyngeal area for transport. The type of local mucus and its role in aggregating small particles into clusters for facilitating transport is discussed in Sibbing et al. (1984). The spatial and functional separation of the branchial sieve and the postlingual organ (Fig. 1) requires such a recollection of particles to the medial area for transport. In most teleosts retractive movements of toothed branchial elements in roof and floor are responsible for transport (e.g. Liem, 1973; Lauder, 1983). Neither analysis of the X-ray movies of the carp nor activity in the retractor muscles of the pharyngeal jaws (Sibbing, 1982; Fig. 15) support such a mechanism in the carp. Only the pharyngeal jaw movements may aid in transport of long preys through the chewing cavity (Fig. 3b). The slitlike configuration of the pharynx, essential for selection, almost necessitates a peristaltic type of transport system.

Limitations (cf. Table 4). The lack of opposed toothed elements seriously limits transport of long and struggling food (e.g. filamentous algae, macrophytes and fish) in cyprinids. Earthworms elicit frequent repositioning for transport and long worms (>8 cm) are often spat to improve the grip by re-intake. The maximal distance between chewing pad and pharyngeal teeth will obstruct entrance of food items larger than ca. 3% of the carps body length in diameter.

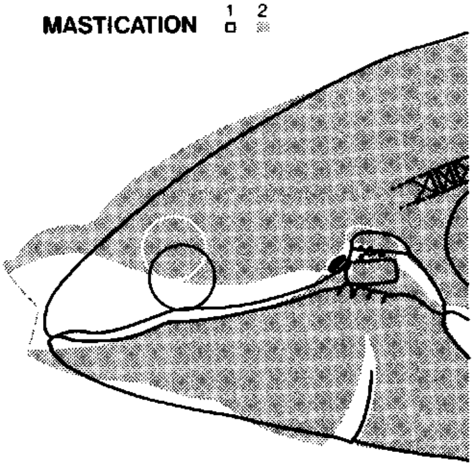


FIG. 11. The power stroke of mastication is characterized by extensive overall expansion of the head and elevation of the skull. The mouth is terminal and opened widely, whereas protrusion is limited, unless loss of suspended particles makes closure by protrusion necessary. Particles are successively crushed and ground. The palatal and postlingual organ hold the food to be masticated and prevent escape of particles to the anterior pharynx. The flow of water through the head is small and slow. Sequence of images at the top.

Mastication. (Fig. 11)

Mastication of large particles generally proceeds as a continuous long series of crushing and grinding cycles (cf. Fig. 3). The skull is lifted in each powerstroke, transmitting high forces of the epaxial body muscles to teeth and chewing pad.

Retraction of the pectoral girdle by the hypaxial bodymuscles plays a similar important role. Direct masticatory muscles that suspend and connect the pharyngeal bones steer and stabilize the masticatory movements (Sibbing, 1982). The posterior parts of palatal and postlingual organ clamp the food to be masticated in front of the chewing pad (Fig. 3; Plate Vb) and obstruct the passage of ground food to the anterior pharynx.

The extensive expansion of the orobuccal cavity which is essential for the grinding stroke effects the opening of the mouth as a consequence. Due to the slow expansion (compare Plates II and V) and the variable opercular abduction, often only increasing at mouth closure and with open valves, this movement pattern does not effect efficient suction (0.5-1 kPa). When suspended food (e.g. zooplankton or bottom material) is stored in the orobranchial cavity during mastication the lower jaw is less depressed (short LOP bursts) and the mouth actively closed in the powerstroke by protrusion of the upper jaw (Fig. 4). This prevents the loss of suspended food. Thus, whereas mastication after feeding large particles is readily recognized by the repetitive opening of the terminal mouth at regular intervals, mastication of small particles proceeds with the mouth closed and may well be confused with closed protrusion in selection. In selection it serves a different goal, occurs more irregularly, usually faster and involves less skull and pectoral girdle movements.

The consequences of the powerful and extensive pharyngeal jaw and skull movements for respiration and for the functioning of the heart and Weberian ossicles have been discussed in Sibbing (1982). The movement pattern of the head during mastication excludes efficient food intake or selection at the same time.

Limitations (cf. Table 4). Mastication serves comminution, rupturing and puncturing food to facilitate the access of digestive enzyms. It is of major importance in cyprinids, which characteristically lack a stomach and oral teeth. The previous study on mastication of the carp (Sibbing, 1982) showed that the profiles and movements of the horny chewing pad and the opposite teeth allow powerful crushing and grinding, whereas there is no ability for cutting and shearing. The masticatory apparatus is built for transferring high forces to the occlusal surfaces. This allows effective comminution of stiff and brittle hard materials and even soft items of fibrous context, whereas tough and elastic food (e.g. macrophytes, worms) is mainly flattened. Arthopod skeletons will partly be crushed, ruptured and punctured (cf. also Klust, 1940). It should be noted that comminution is not a prerequisite for effective digestion of fleshy prey, as long as enzymes can easily penetrate. Furthermore mastication will enhance autolysis. Macrophytes (e.g. common grass) are only partially affected by locally disrupting their fibrous context, washing out the cells (Sibbing, 1982). Even the grasscarp (*Ctenopharyngodon idella*) which has interdigitating rasping teeth appears to have low abilities for damaging the individual cells (Hickling, 1966). Though grinding will diminute smaller particles, the large area of occlusion reduces the compressive pressures. They are probably not sufficient for effective mastication of phytoplankton and diatoms, due to their small size and often firm coat. Contamination of the food with sand grains may enhance grinding, but the horny chewing pad is relatively soft and will be easily worn. No experimental data are available on the lower size limits for effective comminution of such small hard particles. Neither it is known what particle size or surface fractures are required for effective digestion.

The masticatory apparatus of the carp thus has high abilities for efficient comminution of hard medium sized food items such as mollusks and seeds and low abilities for mechanical breakdown of vegetable matter and fleshy prey (cf. Table 4). In view of the tremendous variation in pharyngeal bones and teeth in cyprinids a closer analysis of their role and effects is required to comprehend their relation with diet and habitat. It is furthermore evident that the food-categories of Table 4 do not simply match categories of material properties. Benthic invertebrates e.g. may include soft small worms as well as molluscs. Detritus comprises decaying material of all categories and is not evaluated separately. This not only renders the evaluation in Table 4 generalized, but also shows that distinctions such as between carnivorism and herbivorism are not adequate for characterizing modes of food handling.

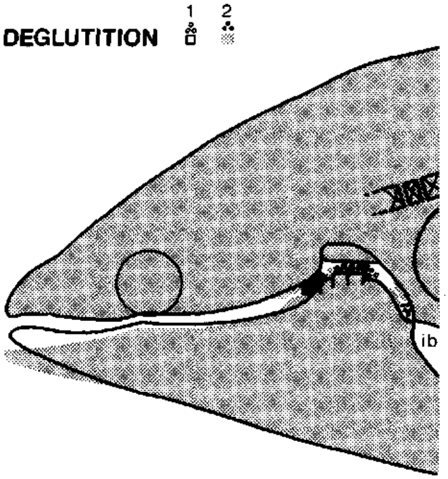


FIG. 12. Deglutition. Ground food is propelled from the chewing cavity towards the esophageal sphincter at the entrance of the intestinal bulb (ib). Deglutition is initiated by the joined activity in the palatal and postlingual organs. This wave propagates through the wall of the chewing cavity into the esophageal muscles. Small movements of the pharyngeal bones aid in transport. Sequence of images at the top.

Deglutition is summarized in Fig. 12 (Sibbing, 1982). The small concomittant stroke of the pharyngeal bone may aid in transport particularly of long objects (e.g. worms, macrophytes) into the esophagus, much like the transport system of a sewing machine. Deglutition will impose no further limitations on food available to the carp than already imposed by transport, loading and mastication. The distensibility of the esophagus should allow passage of particles that already entered the chewing cavity (<3% SL).

Limitations of the adult carp on the exploitation of food

The above survey of movement patterns, their mechanisms, effects and interactions affect the process of food handling as a whole. As food has to match all subsequent restrictions of handling prior to its chemical breakdown the following tentative conclusions are proposed for the carp (cf. Table 4).

1) Retention of phytoplankton and diatoms is restricted to their large-sized fraction (>250 µm) which excludes most species (Moss, 1980). Their use will be further limited by the low ability of the carp for their mechanical breakdown by mastication.
2) Use of long filamentous algae and vascular plants is limited by their intake, and transport, whereas damage to hard single cells by mastication will be small. Purification is restricted. Small thallose algae may well be taken.
3) Zooplankton (>250 µm), benthic invertebrates (<3% SL diameter) and surface floating insects are effectively handled.
4) Exploitation of fish is excluded for the carp due to their escape at intake and their struggling at transport. Large fish (>9% SL predator in diameter) can not even enter the mouth. No devices for laceration are available.
5) Only coarse detritus (>250 µm) is retained by the fish and is further handled with varied effectivity, depending on its component parts belonging to previous categories. It is largely composed of vegetable matter (Darnell, 1964).

These conclusions largely match the actual diet of the carp qualitatively (see page 138 and Sibbing, 1982) and support its wide though limited array of feeding potentials. The fish appears however much less able to handle vegetable matter efficiently, excluding seeds, than animal prey. No reports on the presence of cellulases in the intestinal juices of the carp have been found. They occur only rarely in other fish (Fänge and Grove, 1979). This compilation renders the herbivorism of the carp

FOOD TYPES AND THE ABILITIES OF THE ADULT CARP TO PROCESS THEM EFFECTIVELY

Food handling elements / Trophic categories**	detection (ext.+int.)	intake	retention*	transport loading	mastication	suitability as food
phytoplankton (<250 µm)	+	+	−	+	− ?	−
benthic diatoms (<250 µm)	+	+	−	+	− ?	−
filamentous algae	+	±	+	−	±	−
vascular plants an thallose algae	+	short ±<9%SL	+	±<3%SL	±	±
detritus	+	+	+>250µm	+		
zooplankton	+	+	+>250µm	+	+	+
benthic invertebrates	+	+<9%SL	+	+<3%SL	+	+
aerial insects	+	+	+	+	+	+
fish	+	−<9%SL	+	±<3%SL	−	−

* Purification ability decreases with increasing surface area of the food.
** Hyatt (1979) for aquatic feeding.

TABLE 4. Tentative limitations in food exploitation due to the separate components of the feeding sequence. Measures refer to the smallest diameter of the food. SL refers to the standard length of the fish. Measures of retention belong to carps between 150-1500 gr. (Uribe-Zamora, 1975). Further explanation in text.

doubtful in terms of efficiency. It may well be explained by abundance of vegetable food and scarcity of animal prey. Besides such herbivorism may focus on the ingestion of small animals living on and between macrophytes. The quantitative food exploitation pattern will largely vary and depends on the availability and abundancy of the separate food categories. Abundancy of varied gastropod molluscs even results in positive intratrophic selection of unsculptured thin shells (Stein, Kitchell et al., 1975), which are readily crushed. The final choice of a fish is expected to be a compromise between availability, energy costs-gain ratio and handling time (see below) of a particular food type. Search, detection and predation strategies play a substantial role in the overall efficiency of feeding.

Many of the above hypotheses need further experiments to detail the above limitations, combined with a refined analysis of the carp's ethology and ecology.

BEHAVIOURAL ADJUSTMENTS IN FOOD PROCESSING AND HANDLING TIME.

Feeding sequences differ according to the type and purity of the food (Figs. 3,4; Table 2). They are composed of distinct and often alternative elements, incorporated in a programmed order (Fig. 13). The composition of the feeding sequence will reflect its adjustment to changing external (environmental, oropharyngeal) and internal stimuli (drive or motivation).

The distinct elements of feeding behaviour may well be considered as fixed action patterns i.e. stereotyped and readily recognized units of behaviour (Baerends, 1971). Like in non-behavioural characters there is some variability. The stereotyped component of the pattern (e.g. particulate intake) is triggered by external stimuli (e.g. stimuli of the food), the orientation component (cf. Baerends, 1971) steers the activity according to external cues (e.g. direction of protrusion). Repositioning, back-washing and recollection from the branchial sieve have been distinguished by their effect on the food. These elements are however expressions of the same action pattern i.e. closed protrusion. In the electromyograms they were all consequently referred to as positioning, because the events of the food were not always recorded. Closed protrusion seems to be a core motor pattern (cf. core function in Barel, 1983) common to a more complex set of functions in feeding. Internal factors determine the drive or motivation for feeding and cause variation in the release threshold for the patterns. Thus an increased drive for feeding due to persistent lack of animal prey may lower the threshold for feeding on vegetable matter and increase the tendency for the consuming act. Combination of external and internal factors determine if and what food is chosen and how it is further handled.

When feeding is interrupted by spitting and immediately followed by re-intake of other particles, which often occurs at bottom inspection, this is considered a searching sequence extended into the oropharyngeal cavity and referred to as 'probing' (Fig. 13), an appetitive behaviour largely driven by internal factors. Spitting also occurs as a ultimate rejection pattern involved in search for food. It may even be used quite differently by exposure of hidden food through a jet of water at searching.

The releasing, maintenance and stopping of the component action patterns, their adjustment to the momentaneous situation of particles and their integration into an effective feeding sequence requires refined sensory and regulatory mechanisms and probably involves positive and negative feedback loops. The enormous differences in handling different types of food (Figs. 3,4) show the uniformity of the constituting movement patterns but also the considerable differentiation at

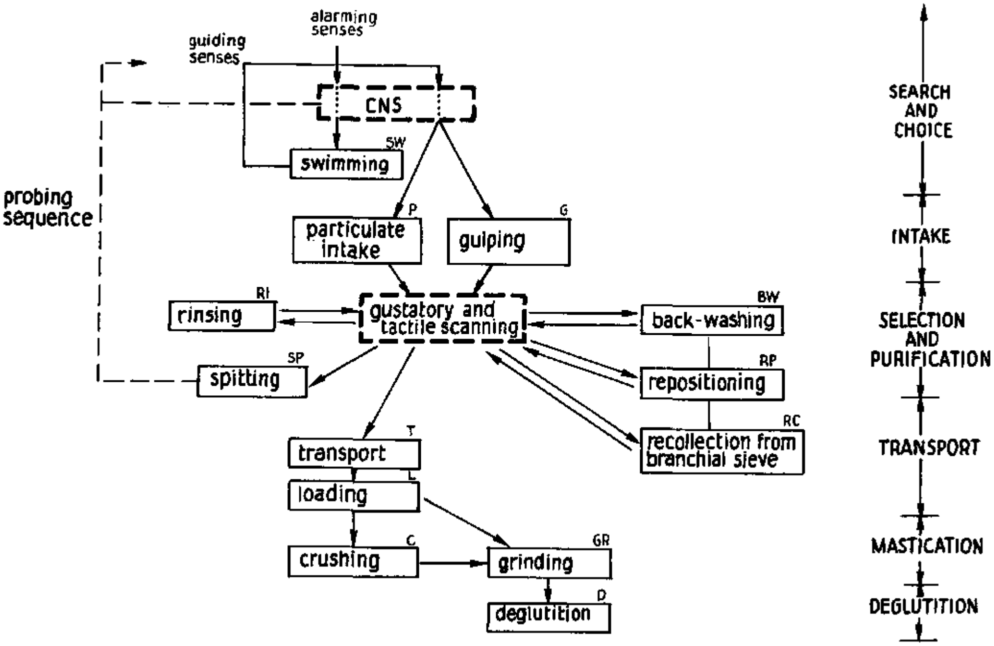


FIG. 13. Interrelations between the distinct elements of food handling. These stereotyped patterns are integrated into effective feeding sequences adjusted to the type of food (cf. Table 2). Probing refers to the repetitive particulate intake of bottom-material for inspection without completion of the feeding act.

the level of the individual muscle activity. The great variation in the palatal activity is an other example.

Handling time is an important parameter for feeding efficiency and should include the total time spent in food processing. The electromyograms of feeding sequences for different food types show considerable differences in handling time. Whereas handling time for a large particle is long and largely determined by mastication, suspended and soiled food require more time for respectively intake and selection (Figs. 3,4; Table 2). The time needed to handle equivalent volumes of food depends on the food properties (e.g. grains of barley takes often several minutes; Sibbing, 1982). It will be short for large pure items. The use of electromyography for analyzing handling times and the determination of food volumes taken could further test such hypotheses.

GENERAL DISCUSSION

Retracing the cyprinid feeding mechanism

Detailed analysis of food handling revealed ten stereotyped action patterns and involves a considerably higher differentiation than already demonstrated for euteleosts (cf. initial strike, buccal and pharyngeal manipulation, and pharyngeal transport (Lauder, 1983)). Though this analysis applies only to the carp, it nevertheless raises the question how such a complex biological design could have evolved among the lower teleosts. No knowledge on fossils of the Cypriniformes exists (Roberts, 1973). Fink and Fink (1981) recently provided a cladogram of the groups of Ostariophysean fishes about the interrelation between cyprinoids and the other suborders. Historical data about the origin of their feeding mechanisms are lacking. The present morphological and functional knowledge can be used to reconstruct a possible evolutionary scheme.

The cyprinoids (Cyprinidae and Catostomidae) share, among others, the following unique characters (Roberts, 1973).

1) A protrusile mouth, comparably specialized as in Acanthopterygii.
2) Toothless jaws.
3) Tootless palate
4) No upper pharyngeal elements of the fifth branchial arch.
5) Enlarged fifth ceratobranchials.
6) Basioccipital bony processes uniting below the aorta.
7) Exceptionally deep subtemporal fossae.

The palatal organ appears similarly shared by cyprinoids and few other fishes, the allied Cobitidae and some Salmonidae) (Kapoor et al., 1975).

The general primitive euteleostean pattern from which the Cypriniformes deviated shows a grasping type of dentition on small tooth plates fused to the oral jaws and upper as well as lower branchial elements (Nelson, 1969). These branchial elements commonly function in seizing and swallowing prey as mentioned above (Lauder, 1983) and belong mostly to predaceous fish with a well developed prehensile and a simple selective apparatus. A plausible tentative scheme for the development of the unique character-set of cyprinids could be visualized as follows.

Cyprinid ancestors could have chosen the bottom areas, using the hitherto rather unexploited vegetable matter as food. Recent cyprinids comprise a large proportion of herbivores compared to other teleost families (Howes, 1978). The hard and fibrous consistency of plant material requires higher masticatory pressures for reaching the cell contents than fleshy prey does. This could have induced a hypertrophy of the fifth branchial arches and their associated muscles. A specialisation at this location would little interfer with respiratory functions of the branchial basket. Their posterior position furthermore allowed the unique insertion on these pharyngeal jaws of a sphincter oesophagi derivate, the retractor dorsalis muscle (Holstvoogd, 1965), thus further increasing masticatory abilities (cf. Sibbing, 1982). Another drastic change in this region of the skull is the vast subtemporal fossa containing the massive levator muscle of the lower pharyngeal jaw. The reduction of movable upper pharyngeal elements may wel be explained by their limited ability to resist the high forces thus produced. Cornification of the pharyngeal epithelium and the underlying occipital region of the skull now serve in absorbing the high masticatory forces. The functioning of the skull base as occlusal surface in mastication forms part of this key-adaptation in the chewing apparatus, and even permits epaxial body muscles to transmit their large forces effectively to the chewing pad.

The role of the pharyngeal masticatory apparatus may well have released the oral jaws from their biting function. Reduction of the associated need for a firm upper jaw abutment could well have allowed the development of the unique kinetics in the cyprinid mouth apparatus (cf. Gosline, 1973) for bottom feeding. The lack of oral grasping teeth might be related to the feeding on immobile soiled prey and probably required space for taste buds on the lips (ca. $380/mm^2$ in the carp, cf. Sibbing et al., 1984), appropriate for bottom inspection. One of the consequences of such structural transformation is the exclusion of piscivory, as fast and struggling large prey can not effectively be taken nor transported, due to the reduction of posterior upper pharyngeal toothed elements. Predators are rarely met among cyprinids. Hypertrophy of the pharyngeal wall into the palatal and postlingual organs provides a substitute for the transport function, lost with the upper pharyngeals. Their sensory and effector abilities (cf. Sibbing et al., 1984) and the closed protrusion pattern of movement are crucial in selection between food and non-food and characteristic for cyprinids as well as catostomids. Due to protrusion volume changes in the oral cavity increases in the carp for manipulating the flow of particles whereas volume changes in the pharynx are reduced in the carp for maintaining a large contact area at selection. Even if such a scheme for the origin of the cyprinoid feeding mechanism proves to be incorrect it still provides a frame for understanding the interrelations of their unique set of characters. These structures are intimately functionally linked and together provide the complex requirements for the subsequent movement patterns in feeding actions. In such a view the piscivorous cyprinids are not the primitive members of the family but are secondarily derived from bottomfeeding species because the above sequence of events explains the early loss of characters appropriate for piscivory.

Protrusion

The important roles of premaxillary protrusion in food handling of the carp may be summarized shortly. 1) Protrusion directs the suction flow to a small area in front of the mouth opening. It increases the velocity of flow through the reduced aperture of the mouth, allowing dense, distant and less accessible food to be taken. 2) By extending the length of the mouth, protrusion simply reduces fish-food distance without adding impulse to the water or the fish. 3) Ventrad protrusion maintains a wider field of vision at bottom feeding and facilitates rapid escape from predators. 4) Protrusion allows the aiming of the fish at the food without the need for a sudden change of the body. This permits prey suction under variable small angles with the body axis. 5) This furthermore allows continuous probing of the bottom substrate while extending the search area by swimming. 6) Protrusion effects a rostral hood at mouth closure during gulping thereby maximizing the volume taken and preventing the loss of suspension. 7) Closed protrusion aids in resuspension of food particles in the orobuccal cavity, essential for the internal selection and purification of food. 8) Closed protrusion allows particles to be washed back for repositioning and recollection from the branchial sieve.
Whereas the first four advantages of protrusion for particulate feeding in the carp have been noted previously for other teleosts (cf. Alexander, 1970; van Leeuwen and Muller, 1984; see Motta, 1984), the latter roles have been unknown but are of crucial importance in bottom feeding on mixtures of food and non-food. Thus the contribution of protrusion to mechanisms for internal selection may have added to the accessibility of the bottom substrate as a possible food source in cyprinoids.

The comparison of structure and functioning within several trophic types of cyprinids (and other cypriniforms) is important to provide more data about the above tentative scheme. The elegant comparison between trophic specialists in cichlids by Barel (1983), though by its wide comparison necessary limited in its analysis of functions, provides a promising example of the impact that feeding habits may have on the constructional morphology of fish.

Detailed and quantified knowledge of the feeding mechanisms and structures combined with the ecological and ethological details of sympatric species will aid in predicting the probable effect of habitat changes for the natural fish fauna.

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HOOFDSTUK 3

REGIONAL SPECIALIZATIONS IN THE ORO-PHARYNGEAL WALL AND FOOD PROCESSING IN THE CARP (*Cyprinus carpio* L.).

F.A. Sibbing and R. Uribe

SUMMARY

The structure of the oro-pharyngeal wall of the bottomfeeding common carp is investigated using light-and scanning electron microscopy. Densities of taste buds, mucus, club cells and the thickness of muscular layers are measured. Distribution patterns of these elements over the oro-pharyngeal surface are reconstructed from local counts. Six areas characterized by a specific combination of morphological features are distinguished and related to twelve movement patterns composing the process of food intake and handling in the carp. These areas are the lips (detection and oral manipulation of food), the orobuccal cavity (suction and resuspension chamber of ingested food and non-food particles), the most anterior pharynx (coarse selection of large food particles), the lateral pharynx (selection of small food particles), the posterior part of the anterior pharynx (formation of boluses, transport and loading of food into the chewing cavity) and the posterior pharynx (mastication and deglutition), The conical shape of the orobuccal cavity and the slit-shaped anterior pharynx reflect two different mechanisms for particle handling viz. by suction and by muscular bulging respectively. The opercular cavities serve large volume changes for suction feeding.

Protruding types of taste buds and oligivillous epithelial cells may well serve mechanoreceptive functions required for steering the process. Otherwise, specialized mechanoreceptors have not been recognized. Mucous cells producing low-viscosity sialomucines occur in the anterior part of the oro-pharynx. They will serve maintaining a laminar flow during suction and lubrication of particle handling in the pharynx. Epithelial microridges may aid in holding the mucus. High-viscosity sulfomucines only appear in the posterior part of the pharynx and will aid in trapping small particles and sticking them into boluses. The commonly accepted alarming function of club cells and their meachanism for release is questioned in view of their abundancy in the orobuccal cavity.

The structure of the muscular palatal organ is discussed with respect to its role in selection between food and non-food particles. The available information on the afferent, efferent and central neural pathways of this system is briefly reviewed. Three levels of movement, related to the particle size to be handled, are proposed. Movement of the palatal organ as a whole, local outbulging of its surface into the pharyngeal slit and a possible very local movement of the muscular papillae in its anterior part. These hypotheses are based on the almost maximal taste bud densities (820/mm^2) in the palatal organ, the known complex laminated cyto-architecture of the enormous vagal lobes processing its input and suggestive of a palatotopic mapping, and on the complex muscle fiber systems in this organ. The movable gill rakers of the branchial sieve, each supplied with a muscular pad and numerous taste buds (325-625/mm^2), suggest their additional active role in selection.

Muscle fiber systems in the posterior part of the palatal as well as in the closely appressed postlingual organ serve a peristalsis-like transport to the chewing cavity. Both are copiously supplied with sulfomucines from their deep crypts.

Together these morphological and physiological features allow the carp a bottom feeding behaviour requiring the effective separation of food from soiled mixtures.

Contents

INTRODUCTION

The trophic diversity among cyprinids stimulated many studies on the adaptive characters in the alimentary tract of this largest teleost family. Suyehiro (1942) and Kapoor et al. (1975) have presented reviews on this subject for teleosts in general. Verigina (1969) has done so for cyprinids. Structural data on the carp are reported by Curry (1939) and Al-Hussaini (1949). In the last decades new techniques revealed additional types of specialized sensory and secretory structures in fish epidermis (cf. Whitear, 1971; Fox et al., 1980; Mittal et al., 1980).
Bottomfeeding cyprinids suck mixtures of food, detritus and inorganic materials with their toothless protrusile mouth. Afterwards they select between food and non-food within their oro-pharyngeal cavity. The muscular palatal organ in the pharyngeal roof, most developed among cyprinids in the carp (Weber, 1827; Herrick, 1904; Dorier and Bellon, 1952) and even larger in catostomids (Weisel, 1962; Eastman, 1977), is a conspicuous cyprinoid feeding structure. Its size, complicated structure and abundant taste buds has led to a variety of hypotheses about its role in food selection and respiration (cf. Kapoor et al., 1975). Its innervation by a huge vagal lobe in the brain furthermore suggests an important role in feeding (Evans, 1952).

The lack of a functional analysis of the actual events during feeding limited the explanation of the varied structural components as adaptive characters. Therefore previous papers on the common carp present an analysis of the feeding mechanism using electromyography, light and X-ray cinematography (Sibbing, 1976, 1979, 1982; Sibbing et al., 1984). The feeding sequence of this species appears to be composed of twelve stereotyped movement patterns serving intake, selection, transport, mastication and deglutition. The feeding sequences are adjusted to the location, size, movement, contamination and consistency of the food by the appropriate employment and repetition of these specific movement patterns.

The aim of the present study is to analyze the sensory and effector structures in the oro-pharyngeal wall which determine the efficiency of internal food processing. To understand the structure-function relationships the macroscopical and (electron) microscopical morphology of the oro-pharyngeal wall are related to the actual events during feeding. Details of taste buds, oligovillous cells, mucus, microridges and muscle fiber arrangment can now be fitted in one comprehensive view of food handling and food processing. As the functional differentiation is now known into great detail also quantitative measurements of the above elements and their reconstruction into distribution patterns are required to establish form-function relationships. For example, disagreement between Curry (1939) and Al-Hussaini

(1949) on the presence and number of particular cell types and taste buds in the carp is largely due to their inadequate descriptive terms.

The present data and a critical review of carp feeding show a considerable gap in our knowledge. This concerns mainly the lack of information on the presence and properties of the involved sensors and the way the fish manages to integrate and use their enormous input to regulate its feeding behaviour. We hope this study to be a stimulating factor for such research. Another aim of this study is to provide a general frame for comparing feeding in cyprinid species. This will improve our insight into the trophic segregation of cyprinid species living together in one community.

MATERIALS AND METHODS

All mirror-carps (*Cyprinus carpio* L.) were reared in our laboratory and fed on small Trouvit grains (Trouw and Co., Putten, The Netherlands).

Histology

For histological examination descaled carps of 58 mm SL were fixed in Bouin's fluid (Romeis, 1968) and decalcified over two weeks in a mixture of 200 ml formic acid, 200 ml ethanol (70%) and 40 gr. sodiumcitrate, renewed every three days. After dehydration over a graded ethanol series the specimens were embedded over amylacetate in paraffin. Serial sections of the head (7 µm) were stained after Crossmon (Romeis, 1968) allowing a clear distinction between connective tissue, muscle fibers, mucous cells, club cells and taste buds.

Neutral as well as acid mucus is stained with Periodic Acid Schiffs reagens (PAS; McManus et al., 1963). Acid mucopolysaccharides and glycoproteins have been localized by positively staining with Alcian Blue (AB) at pH 2.5 (McManus et al., 1963). A reaction with High Iron Diamin (HID; Spicer, 1965) further distinguished acid sulfomucines (pos. staining) from acid sialomucines (neg. staining).

Morphometry

Four parameters were measured at 980 µm or smaller intervals through the length of the oro-pharyngeal cavity (ca. 15 mm).

The density of taste buds was measured by counting in the 7 µm transverse sections each taste bud intersection that was clearly distinct from the common epithelial cells. Because the mean diameter at the centre of the taste bud, measured from different regions, was 32.5 ± 5.1 µm (n=60), the actual number of taste buds in a transverse section was determined by multiplying the number of intersections by $7/(32.5 + 7)$ (Abercrombie, 1946). From this number the density of taste buds per mm^2 oro-pharyngeal surface was calculated. The surface was measured as its projection on a horizontal plane, thus not accounting for folding of the epithelium. The head elements were in a resting stage (cf. Plate IId). As the pear-shaped taste bud (height 44.0 ± 7.5 µm, n=60) was considered as a globe in the calculations, their number may be an over-estimation, due to the inclusion of intersections of their extraglobular top. Such intersections are scarce because taste buds were generally cut sagitally. Similar measurements of a second carp of the same size and origin gave an identical distribution pattern. The absolute number of taste buds was however about 10% lower.

Whereas taste buds were quantified over large areas (Fig. 1), an accurate determination of the amount of mucus, occurring in several small cell types, requires detailed measurements at high magnification. Therefore only small areas in each cross-section were measured by point-counting all mucous material in the epithelium (7245 points/ mm^2 grid). Thus the longitudinal mucus distribution was determined from a medial 300 µm width area (Fig. 1). So a relative measure for the mucus in this medial tissue strip is obtained, irrespective of the size or number of mucous cells and their secretion kinetics.

The muscle layer development over the length of the oro-pharynx was determined by measuring its thickness in the median of the fish. Due to shrinkage by fixation these values are low compared with a fresh carp.

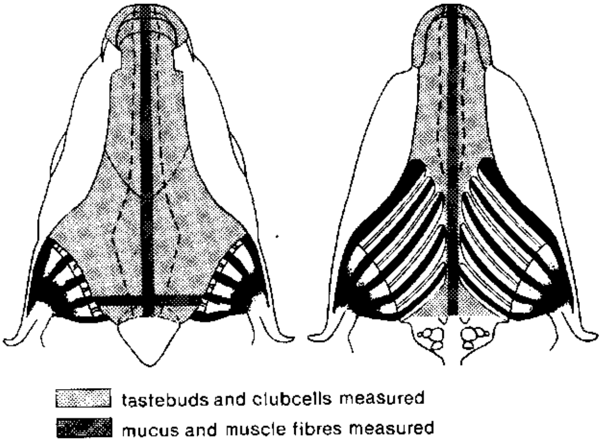

FIG. 1. Roof (left) and floor (right) of the oro-pharyngeal cavity of a carp, indicating the areas used in quantifying taste buds, club cells, mucus and muscle layers. The pecked line marks subdivisions measured.

The density of club cells was determined by counting the number of their intersections over large areas (Fig. 1). These are expressed per horizontal millimeter transverse section. Only those intersections of club cells were counted which had the unmistakable central nucleus as a characteristic. So the numbers in the graphs provide a relative measure of their intersections, the actual number being higher.

Detailed measurements of taste buds, mucus and muscle layer over the full width of the pharyngeal roof have been made in the posterior part of the palatal organ (Fig. 1) where a varied transverse distribution was most conspicuous. Furthermore, transverse differences in taste bud densities at other sites have been inferred from comparison between counts of the total and the medial areas (Fig. 1). As at the level of the branchial arches and the chewing cavity an accurate measurement of the surface is impossible, data on these areas have been estimated from the SEM photographs and from the microscopic slides respectively (dotted lines in the figures).

Semi-quantitative measurements by distinguishing four density levels of taste buds, mucous cells and club cells in an older carp (SL 20 cm), prior to accurate counting in sections of small carps (SL 58 mm), provided a corresponding picture of their distribution.

Scanning electron microscopy

For scanning electron microscopy (SEM) carps of similar size (53-58 mm SL) were decapitated after anesthesia by an overdose of 200 mgr MS 222/liter (Sandoz, Basel). The specimens were carefully washed in buffered physiological saline to remove mucus adhering to the surface and fixed for eight days at 5^0 C in 3% glutaraldehyde, buffered at pH 7.2 in 0.1 M sodiumcacodylate containing 2.5% glucose (Reutter et al., 1974). Subsequently the heads were cut horizontally in a dorsal and ventral half, each reduced to a slice of few millimeters to fit in the microscope. This material was washed repeatedly in a buffered saline solution prior to final fixation for six hours in 1% osmiumtetroxide, buffered in 0.1 M sodiumcacodylate. After repetitive washing in the buffer, dehydration in a graded series of ethanol (10-100%) and critical point drying, the specimens were mounted on a stub and coated with a film of gold. For examination a JEOL JSM-35C scanning electron microscope operating at 25 KV and magnifications of 10 - 10.000 times was used. The large specimens could be stored for three weeks over a silica gel without damage.

Though SEM photographs may seem to provide an excellent base for fastly measuring the taste buds densities (they give closely similar results for the buccal roof, ca. 40-50/mm^2) these SEM measurements become increasingly inaccurate

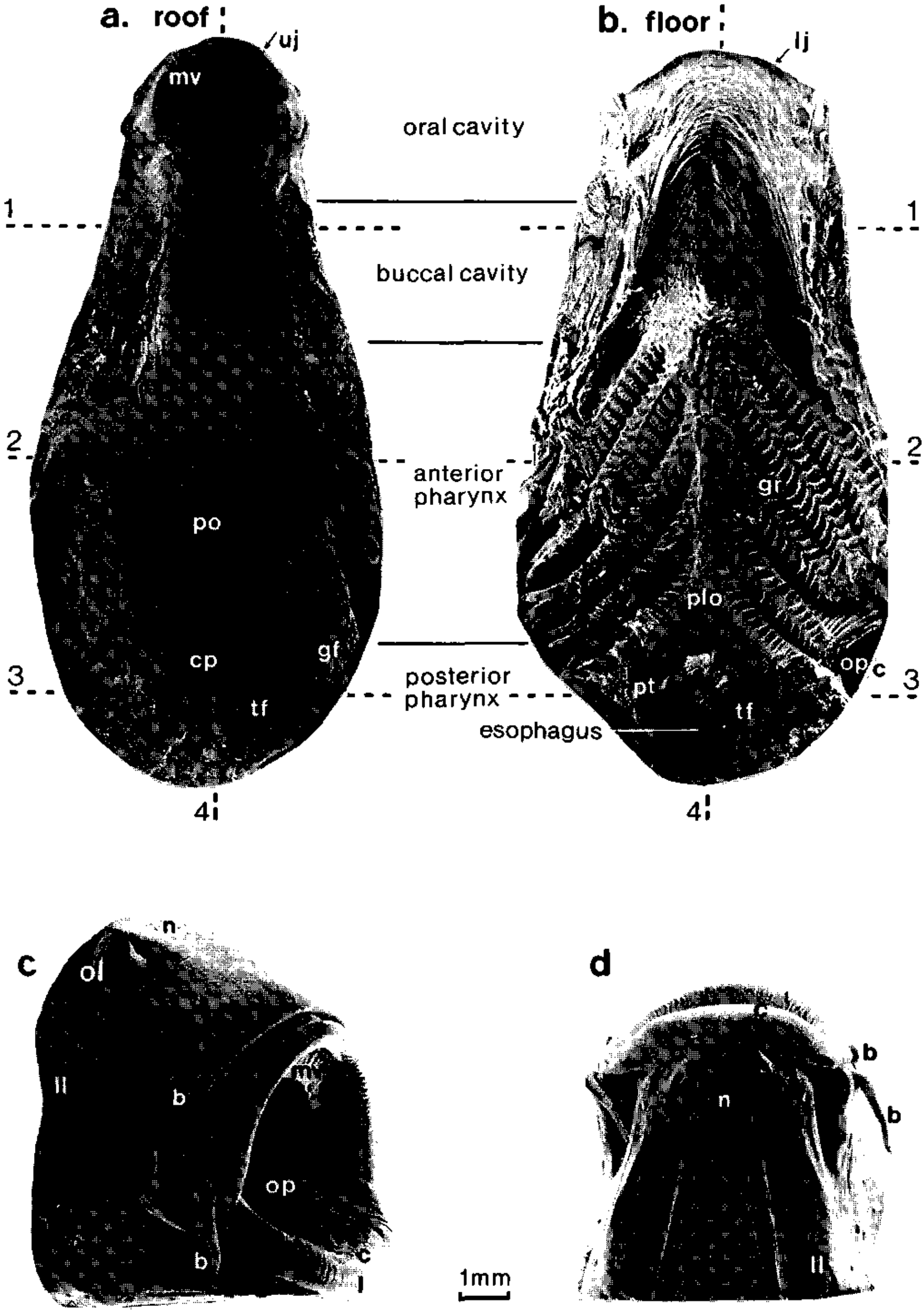

PLATE I. **(ab)** SEM-view on the roof **(a)** and floor **(b)** of the oro-pharynx of the carp (SL 58 mm). Subdivisions of the oro-pharynx are indicated. Levels of sections in Plate IIa-d are given (1-4).

(cd) Fronto-lateral (c) and ventral SEM-view (d) of the snout. Lips (l), barbels (b) and oral lining bear abundant taste buds. The external skin shows conspicuous neuromasts (n), lateral line (ll) and olfactory organs (ol). Abbreviations on page 122.

in posterior folding areas where taste buds are densily packed and protrude less from the surface. Abundant mucus may also render them less conspicuous. Besides SEM techniques do not allow measurements of taste buds as well as mucous cells, muscle fibers and club cells within the same fish.

RESULTS

Gross anatomy

Subdivisions and volume changes in the oro-pharynx.

The *oral cavity* extends from the lips to the level of articulation of the lower jaw, the *buccal cavity* from here to the base of the first branchial arches (Plate I ab).

The pharyngeal cavity in cyprinids is divided into the *anterior pharynx* (syn. branchial cavity) containing the gill arches and involved in respiration and selection and the *posterior pharynx* (syn. chewing cavity) between pharyngeal teeth and chewing pad, involved in mastication (Plates Iab). The respiratory filaments of the gill arches project into the *opercular cavity.*

The maximal diameter of the protruded mouth is about 10% of the standard length (SL) in carps between 10-15 cm. SL. It decreases to about 7,5% for carps of 50 cm. SL. The concave buccal roof and its convex floor (Plate II a) closely fit at compression of the head. During expansion the oro-buccal cavity becomes conical whereas the anterior pharyngeal cavity broadens but remains slit-like, being subjected to minor volume changes (Plate II b). Whereas in a fresh carp the muscular palatal organ almost fully occupies the pharyngeal lumen, its shrinkage by fixation leaves an exaggerated slit in the micrographs. Volume changes in the opercular cavities by far exceed those in the pharyngeal cavity.

Oro-buccal cavity

Snout

The carp bears four maxillary barbels around the terminal mouth (Plate I cd), a lower pair at each jaw angle and a smaller dorsal pair. Each barbel is studded with taste buds, increasing in number towards its free end. Olfactory organs, openings of the lateral line system and free neuromasts are evident on the snout. Few taste buds are found on the skin, as appears from microscopic sections.

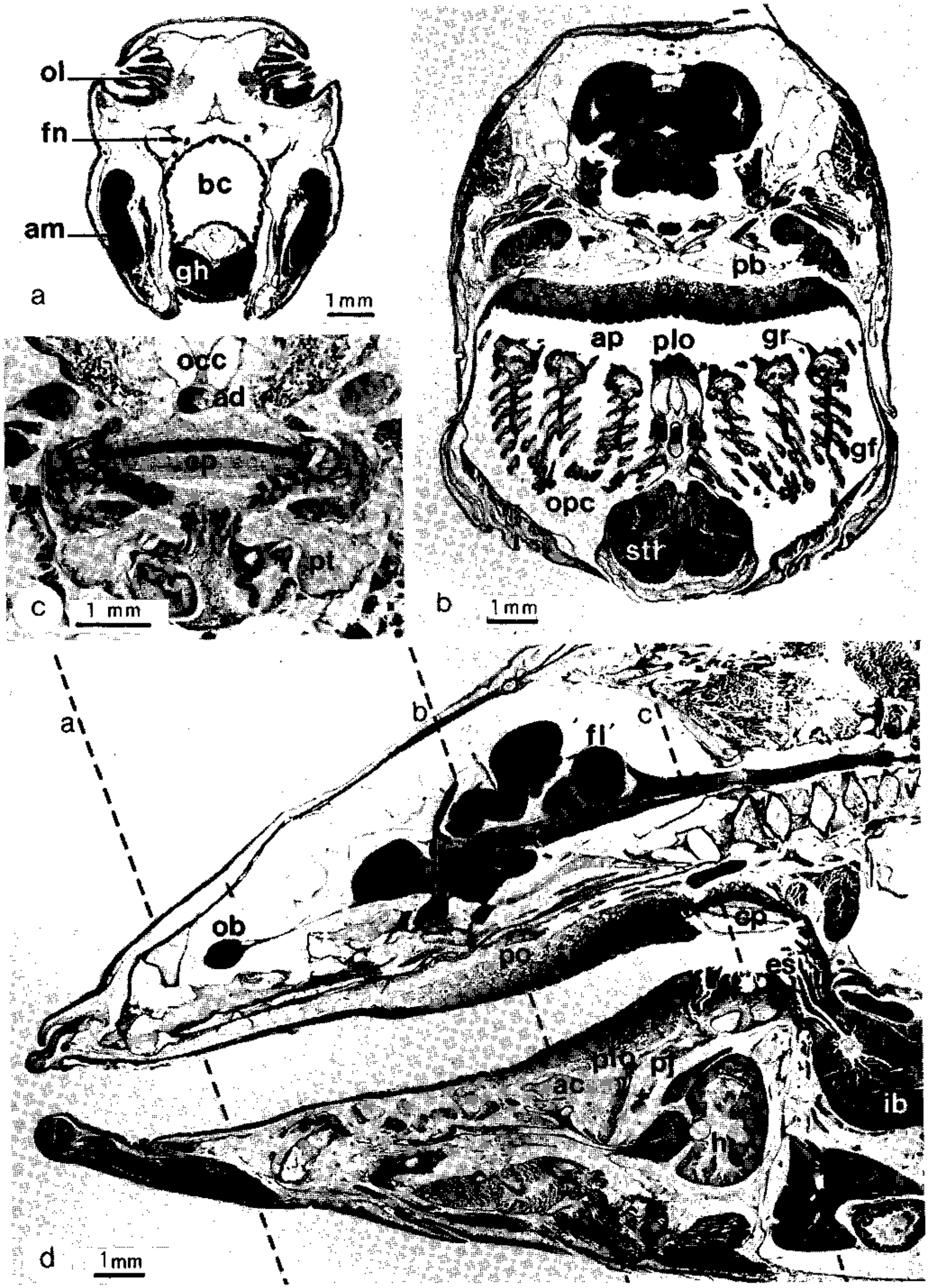

PLATE II. (abc) Transverse sections through the head of a carp (SL 60 mm). Levels are given in Plate Iab and IId. Note the cylindrical shape of the buccal cavity (a) changing into a broad flattened slit in the anterior pharynx (b). The volume of the anterior pharynx is exaggerated due to shrinkage of the palatal and postlingual organ by fixation. The pharyngeal floor is perforated by the branchial slits. The posterior pharynx (c) has a small volume. Note the tissue flaps (tf) projecting between pharyngeal teeth (pt) and chewing pad (cp).

(d) Medial section showing the alimentary tract from mouth to intestinal bulb (ib). Palatal organ (po) and postlingual organ (plo) are conspicuous. Abbreviations on page 122.

The protrusile toothless mouth is bordered by thick lips bearing rows of longitudinally arranged taste buds (ca. 360/mm^2, Plate IIIa) on the flat tops of closely packed epithelial folds. Taste buds are absent at the mouth angles.
Inwards from the lips the taste bud area is interrupted by a small crescent shaped cellular area of cornified epithelium, the area of contact between upper and lower jaw. These horny single cells (Plate IIIa) may be similar to the 'unculi' described for loricarids by Roberts (1982). The cornified area is devoid of taste buds.

Oro-buccal roof

A crescent shaped respiratory valve projects from the oral roof at the inner horny edge of the upper jaw (Plate Iac). Wide papillae (ca. 150 x 200 µm) with abundant taste buds (ca. 250/mm^2) are found in its basal part, its distal half is smooth and taste buds are almost lacking. The roof of the oral cavity is plicated. Anteriorly deep papillated folds run transversad and follow the contours of the protrusile upper jaw (Plate Ia). Behind the jaw articulation buccal plicae run increasingly longitudinally and bear few small papillae (30x40/70 µm, Plate IIIb). Papillae and taste buds (ca. 50/mm^2) merely occur on top of the folds.

Oro-buccal floor

Papillae similar to those on the base of the maxillary valve (ca. 250 tb/mm^2) extend inwards from the horny area of the lower jaw (Plates I b, III a). A mandibular valve is absent. Whereas the transverse folds along the lower jaw are less pronounced, the lower jaw being non-protrusile, longitudinal folds at the level of the cheeks are deep and run caudo-laterad towards the first branchial slit (Plate Ib). These folds allow considerable extension of the buccal walls. Few taste buds lie on their tops (ca. 40/mm^2). The central convex area of the buccal floor, often referred to as tongue, is supported by the mobile glossohyal, connected to the ventral elements of the hyoid arch. A wart-like protuberance marks the posterior end of the glossohyal. Medium-sized papillae (ca. 100x160 µm) with taste buds (ca. 75/mm^2) are conspicuous over all this area.

Pharyngeal cavity

Anterior pharynx

The ***roof*** of the anterior pharynx is formed by a thick muscular cushion, the ***palatal organ***, *covering the base of the skull, the epibranchials and the pharyngo*-branchials (Plate II b). The surface of the slightly bilobed palatal organ closely fits the pharyngeal surface and curvature of the gill arches. Thus the V-shaped

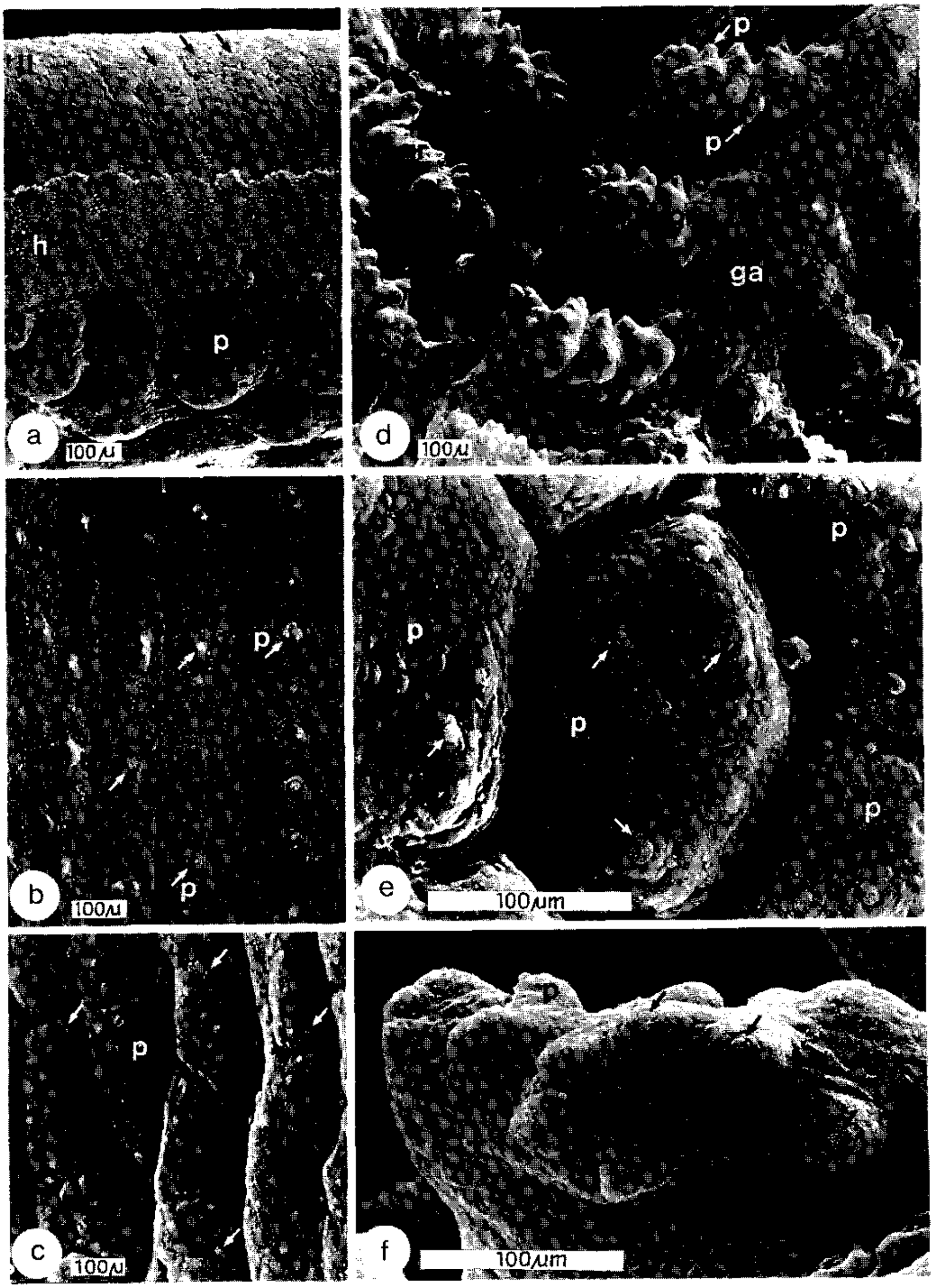

PLATE III. (abcd) SEM-survey of the lower jaw (a), buccal roof (b), anterior palatal organ (c) and gill arches (d).
(a) Rows of taste buds (arrows) on the lips are interrupted by cornified cells at the contact area of the jaws.
(b) Note the few taste buds more or less protruding from the flat buccal roof.
(cd) Their number is increased in the anterior pharynx.
(ef) Details of the anterior pharynx. The lateral part of the palatal organ (e) shows papillae each containing numerous taste buds (arrows). (f) Small conical papillae, each exposing a receptor area of a single taste bud, radiate from a gill rakers. Abbreviations on page 122.

rostral border of the organ follows the attachment of the gill arches (cf. Plates Ia,b) and the organ bends postero-laterally dorsad along with the epibranchials. The slit between roof and floor is broad but narrow and even vanishes close to the chewing cavity in a fresh carp.

The surface of the palatal organ is irregularly but heavily papillated (Plates Ia, IIb, IIIce, IVb) and densily packed with taste buds on the flat tops, even more dense in the lateral areas (average up to 670 tb/mm^2) than in the medial region (av. up to 400 tb/mm^2). Papillae in the lateral areas are smaller (ca. 90 µm diameter) than in the medial region (ca. 140x150/550 µm). In the posterior part of the palatal organ, the triangular area enclosed between the last gill arches and the chewing pad, the papillae lengthen into deep longitudinal folds (Plate Ia, IVc) with a markedly reduced number of taste buds (av. up to 200/mm^2).

The *floor* of the anterior pharynx (Plates Ib, IIb) is largely composed of the gill arches and their rakers. From these plates it is clear that the gill arches and their double rows of rakers form a perforated plane that can be closely applied to the palatal organ.

The pharyngeal surfaces of the gill rakers bear numerous small radiating conical papillae (ca. 30-50 µm diameter), each with a taste bud (av. up to 480/mm^2 in the horizontal part of the gill arches; Plates III df). The tapering gillrakers from subsequent arches interdigitate in a fresh carp and play a role in food selection (Zander, 1906). Between the two rows of gill rakers the pharyngeal surface of each gill arch (Plates IIb, IIId) is covered by a thin muscular strip of tissue with few low papillae and taste buds (ca. 100/mm^2).

The midventral floor of the branchial basket, widening caudally into a triangular area, is covered by the "*postlingual organ*" (after Dorier and Bellon, 1952; Plate Ib, IIb). This fleshly muscular organ is supported by the anterior cartilage (fused basibranchials III and IV), and the pharyngeal jaws (cf. Plate IId). The surface architecture of the postlingual cushion parallels that of the palatal organ in this area (cf. Plate VIIcd). Posteriorly deep longitudinal folds run towards the teeth. Taste buds density in the postlingual organ fluctuates around an intermediate level (ca. 200/mm^2).

The posterior pharynx

The morphology and functioning of the triangular horny chewing pad in the roof and the heterodont pharyngeal teeth in the floor of the posterior pharynx have been subject of a previous paper (Sibbing, 1982). Between the teeth of left and right pharyngeal jaw the pharyngeal mucosa is shaped into protruding foliaceous papillae with few taste buds near their tops (Plates Ib,IIc). Two laterally fixed

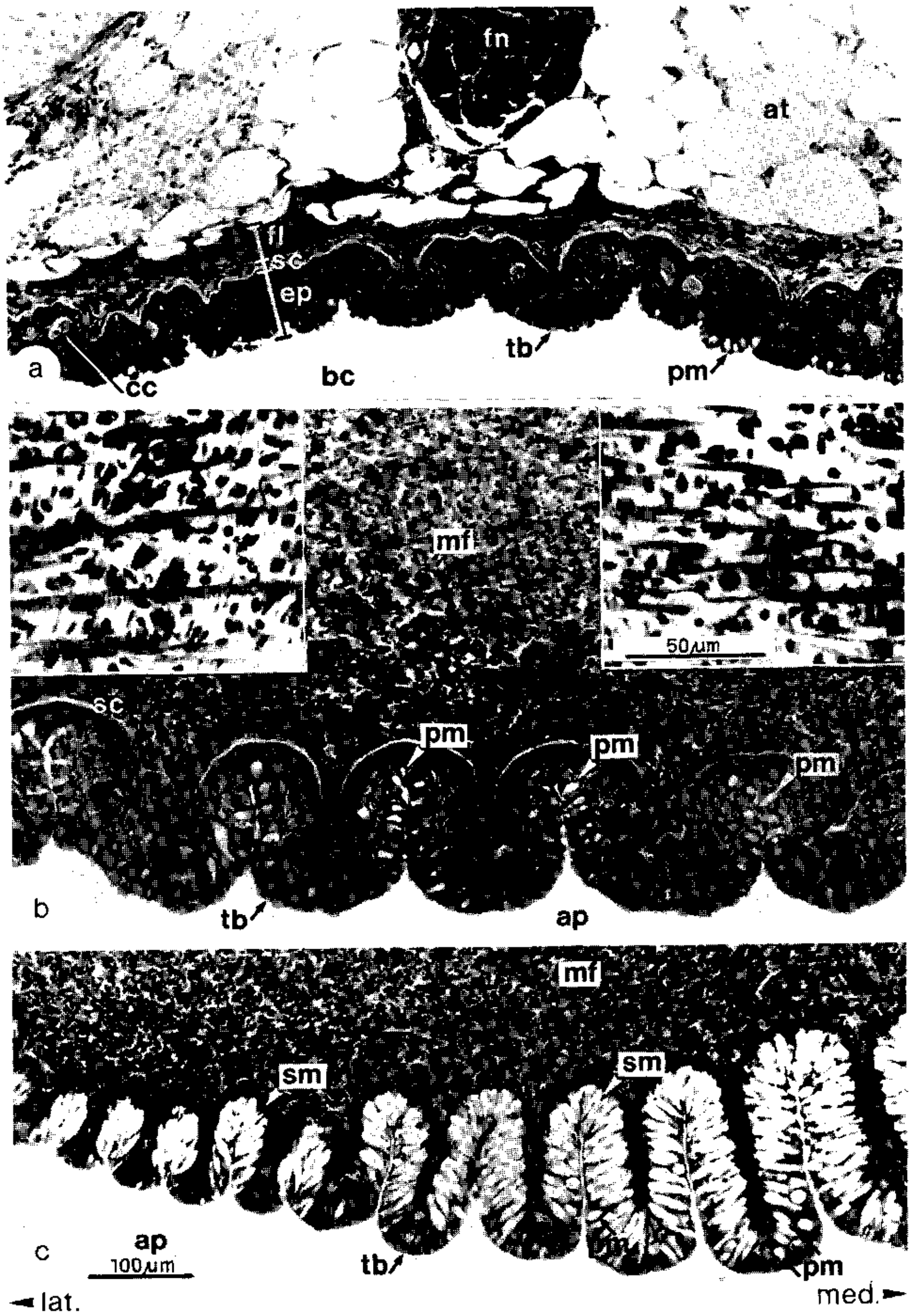

PLATE IV. Transverse sections through the medial area of oro-pharyngeal wall. (a) The buccal roof with club cells (cc) and taste buds (tb). (b) The anterior palatal organ and (c) the posterior palatal organ.

Note the obliquely oriented muscle fibers (mf) in the medial part of the palatal organ. Insets in (b) show their longitudinal and transverse orientation in the lateral parts. Note the large amount of sacciform mucous cells (sm) posteriorly. Abbreviations on page 122.

tissue flaps extend mediad between teeth and chewing pad.
Caudally from the teeth the posterior pharynx tapers ventrad into the, almost vertical, short esophagus, separated from the intestinal bulb by a pyloric sphincter (Plate IId). Cyprinids lack a stomach. Rare taste buds do occur in the first few sections of the plicated esophageal wall.

Light- and scanning electron microscopy of the oro-pharyngeal wall

Tissue layers

The general composition of the *oro-buccal wall* (Plate IVa), being a derivate of the stomodaeum, closely resembles that of the scaleless skin. It is covered by a stratified **epithelium** (50-120 µm thick). The underlying connective tissue stroma consists of 1) **stratum compactum**, a compact coat of collagen fibers (5-7 µm), 2) a less dense **fibrous layer** (10-30 µm) with interposed nuclei of fibroblasts, 3) a loose **areolar connective tissue** with blood vessels and nerves. A distinct muscular coat as reported by Curry (1939) has not been found in the buccal cavity.

The wall of the *pharynx* (Plate IV bc) mainly differs by the gradually vanishing of the stratum compactum and the fibrous layer in lateral and posterior direction. A thick **muscular layer** is now interposed between the fibrous and the areolar connective tissue.

Labels such as lamina propria and submucosa are confusingly used (Curry, 1939; Al-Hussaini, 1949; Eastman, 1970). They have been avoided because they are derived from intestinal nomenclature, which is inappropriate to describe the area between skin and esophagus. A muscularis mucosae, separating the lamina propria and the submucosa in the mammal intestine, is absent in fishes (cf. McVay and Kaan, 1940).

The palatal organ

The pharyngeal walls show conspicuous specializations. The palatal organ has a highly plicated mucous epithelium (Plate IVbc). Taste buds abound on the flat papillar tops, mucous cells dominate along the narrow crypts. The underlying fibers form muscular cores for the papillae and platforms for taste buds. The thick muscular layer backing the papillae is composed of roughly longitudinally and transversely oriented striated fibers. In the medial part of the palatal organ however muscle fibers run obliquely to the body axis (Plate IV b). The scattered fasciculi lie intermingled and gradually merge with the deep layer of areolar tissue. The palatal organ covers the upper branchial arch elements and is at its edges attached to

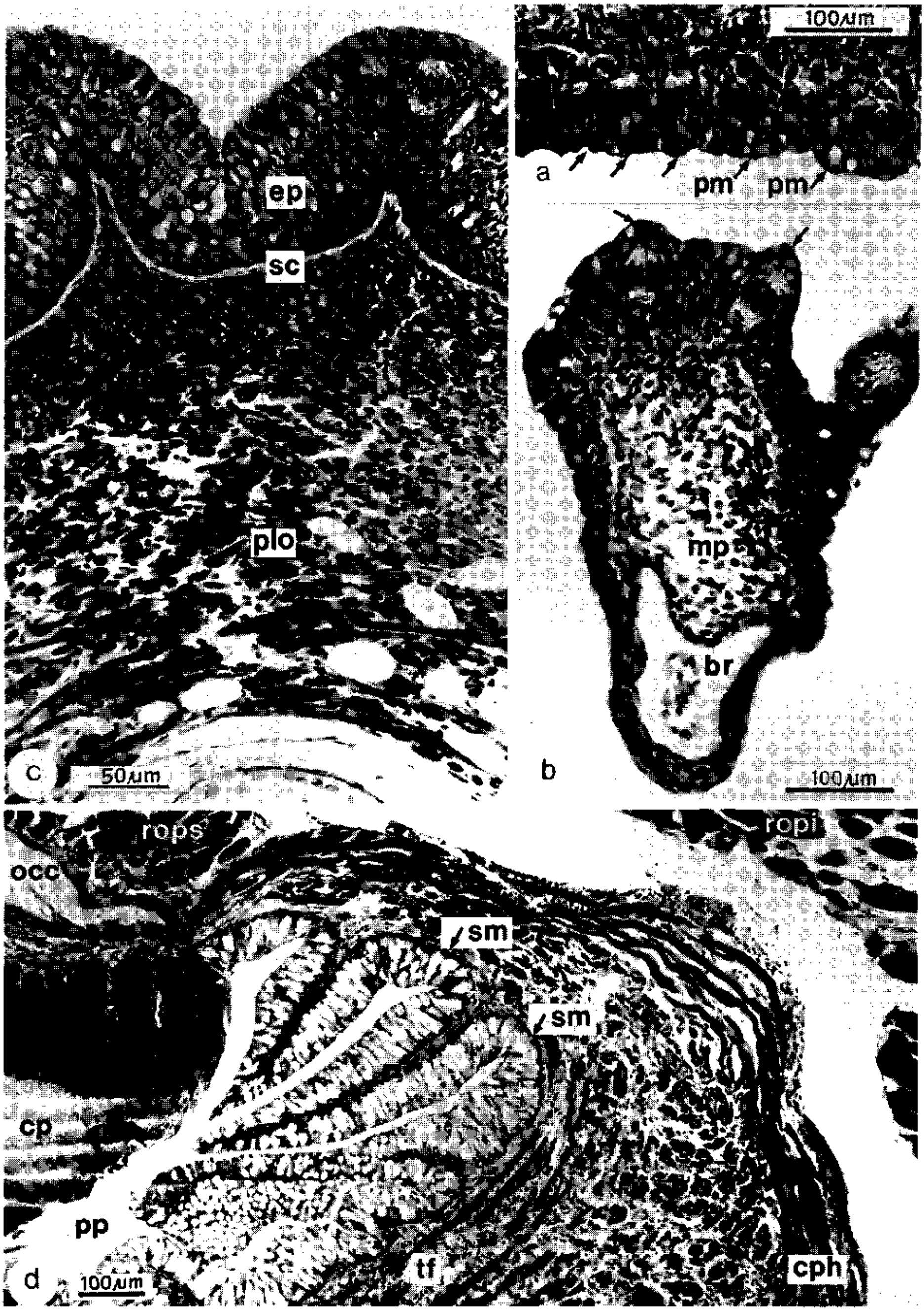

PLATE V. (a) Transverse section through the postero-lateral part of the palatal organ. It is hardly plicated and contains an almost maximal density of taste buds (arrows). Some pyriform mucous cells are conspicuous (pm).
(b) Transverse section through a gill raker bearing taste buds (arrows) onamuscular pad (mp). It is supported by a bony rod (br).
(c) Survey of the medial part of the postlingual organ with the epithelium (ep) at the top, separated by a stratum compactum (sc) from longitudinal and more ventrally transverse muscle fibers.
(d) Transverse section through the dorso-lateral wall of the chewing cavity, showing chewing pad (cp), foliaceous papillae and the constrictor pharyngis muscle fibers (cph) radiating into the lateral tissue flap (tf) (cf Pl. IIc). Some masticatory muscles are at the top of the plate. Abbreviations on page 122.

bony elements and connective tissue plates (Plate IIb,d).

Outwards from the median the papillae (up to 150 µm high) become gradually lower (Plate IIb) and their supporting connective tissue layers decreases from 12 µm to 2 µm. In the posterior medial part of the palatal organ, on the contrary, the papillae lengthen and form high folds (up to 300 µm high) with few connective tissue (5 µm layer). Their small mainly longitudinally arranged muscular core is bordered by abundant mucous cells (Plate IVc).

The postlingual organ and the branchial arches

The medial postlingual organ and the pharyngeal lining of the branchial arches (omitted in the studies of Curry (1939) and Al-Hussaini (1949)), show a similar regional differentiation as the palatal organ and may even be considered to form a tubular entity with it. However, the muscle layer fibers over the branchial arches is thin (cf. Plate IIb) and runs along the length of the arches, oblique to the body axis, whereas it is voluminous in the postlingual organ and runs mainly parallel to the body axis (Plate Vc). Thus the arrangement of muscle fibers in the pharyngeal floor remains oblique with respect to opposing fibers in the pharyngeal roof, despite the regional differences. The functional implications of such a peculiar arrangement is discussed later. The core of the gill raker is supported by a basal bony rod and densily packed with muscle fibers running in various directions, suggesting movability (Plate Vb). The bony rod itself has a fibrous attachment to the branchial arch.

The chewing cavity

The foliaceous mucous lining of the posterior pharynx forms two large lateral flaps projecting between teeth and chewing pad and high branching papillae between and around the teeth (Plates Iab, IIc, Vd). The underlying striated muscles are continuous with those of the esophagus and distinct from the palatal and postlingual organ. They are composed of criss-cross running fasciculi, radiating into the above flaps and papillae, and a peripheral sphincter oesophagi, connecting pharyngeal jaws and basioccipital process.

The roof of the posterior pharynx is formed by the cornified chewing pad (Plates Ia, IIcd, Vd) which is continuously renewed and rests on a thick intruding layer of connective tissue. Its histology has been described by Curry (1939) and Al-Hussaini (1949). Sporadic muscle fibers occur between the chewing pad and the basioccipital process.

The lining of the esophagus closely resembles that of the posterior pharynx, except for the area close to the pyloric sphincter (cf. Curry, 1939; Al-Hussaini, 1949).

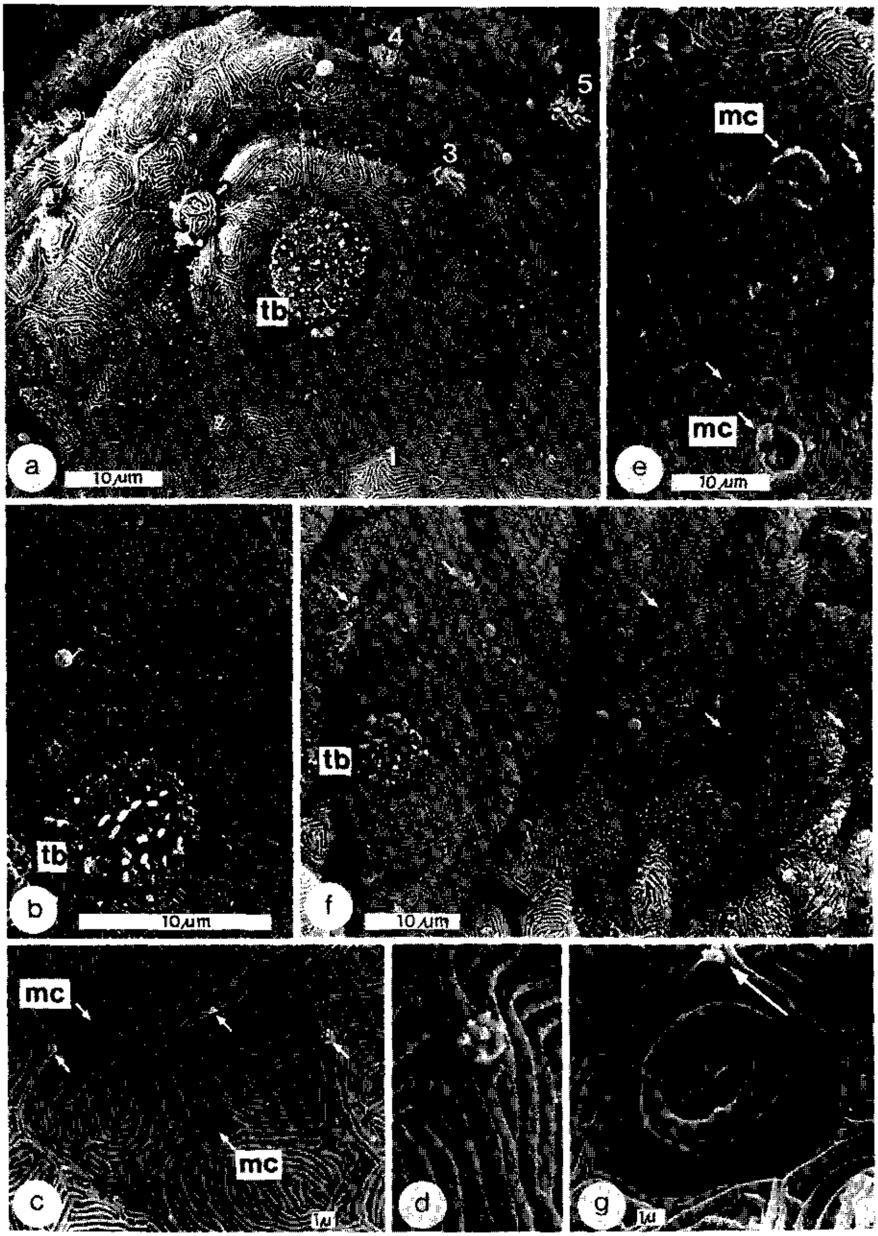

PLATE VI. SEM-views of (a) The edge of a papil from the anterior palatal organ exposing the receptor area of a taste bud (tb), composed of large and small villi. Note the microridge-pattern of the common epithelial cells which cover most of the taste bud. Transitional stages of an epithelial cell suggest cell-sloughing (1-5).

(b) Top surface of palatal folds just in front of the chewing pad. Note the microridge pattern, conspicuously different from (a).

(c) Oral roof area showing groups of small villi (arrows) protruding from between epithelial cells. The smooth apical surface of mucous cells is visible (mc).

(d) Detail of a groups small microvilli from (c).

(e) The buccal floor shows ruptured mucous cells (mc). The membrane-bound mucous packages are exposed. In addition groups of small villi are seen (arrows).

(f) In the area of the teeth bundles of long villi (arrows), different from the taste buds (tb), protrude from the folded epithelial surface. The microridge pattern is intermediate between that in (a) and (b).

(g) Cells widely spread over the internal opercular lining, suggestive of some secretory role. Abbreviations on page 122.

Connective tissue layers are thicker than in the chewing cavity, where they are generally hardly recognizable in the papillae.

Specializations of the oro-pharyngeal epithelium

The stratified oro-pharyngeal epithelium contains specialized cells like horny cells, mucous cells, club cells, chloride cells, sensory cells and 'round cells' as in fish epidermis (Whitear, 1971; Mittal et al., 1980). Their abundancy varies locally and they serve a multitude of functions.

The surface of the *common epithelial cells* (5-10 µm, diameter) is commonly intricately sculptured by *microridges* (Reutter, 1973, 1974; Hawkes, 1974; Hughes, 1979; Mittal and Banerjee, 1980; Ono, 1980). In the carp the microridges (width 0,17 - 0,23 µm) generally have a fingerprint pattern (Plate VI). The bordering microridges of adjacent cells run parallel and leave a narrow space between (ca. 0,05 µm). It is suggestive to interprete the cells 1-5 in Plate VIa as successive stages in the cast off of an old cell.

In life the whole epithelial surface is covered by a slimy and fibrous layer, a cuticle (about 1 µm thick), which is secreted from the underlying common epithelial cells as has been demonstrated by Whitear (1970) in *Phoxinus* and some other teleost fishes. This external coat continues over the aperture of taste buds and mucous cells and is most probably composed of glycoproteins. It was eliminated during preparation of the SEM sample by washing the specimen with buffered saline, and it is frequently lost during preparation of histological sections. The mucus of the mucous cells forms a layer on top of this cuticle (Whitear, 1970).

Local cornification is common among terrestrial vertebrates, not in fish (Mittal et al., 1980). *Horny cells* are found in the carp at the rims of the upper and lower jaw (Plate IIIa) and in the chewing pad (Plate Vd).

Effector specializations

Mucous cells

Mucous cells, usually called goblet cells, are the most common unicellular glands of fish epidermis. They have their secretory product packed in membrane-bound vesicles, which displace the nucleus to the base of the cell (cf. Plates IV, V). During maturation they force the surrounding cells apart (Henrikson and Matoltsy, 1968) and eventually expose their smooth top (diameter 3-7 µm) at the surface (cf. Plate VIce). At rupture of the cell the membranes break down and the mucus is released. Plate VIe shows most probably the surface morphology of partly ruptured

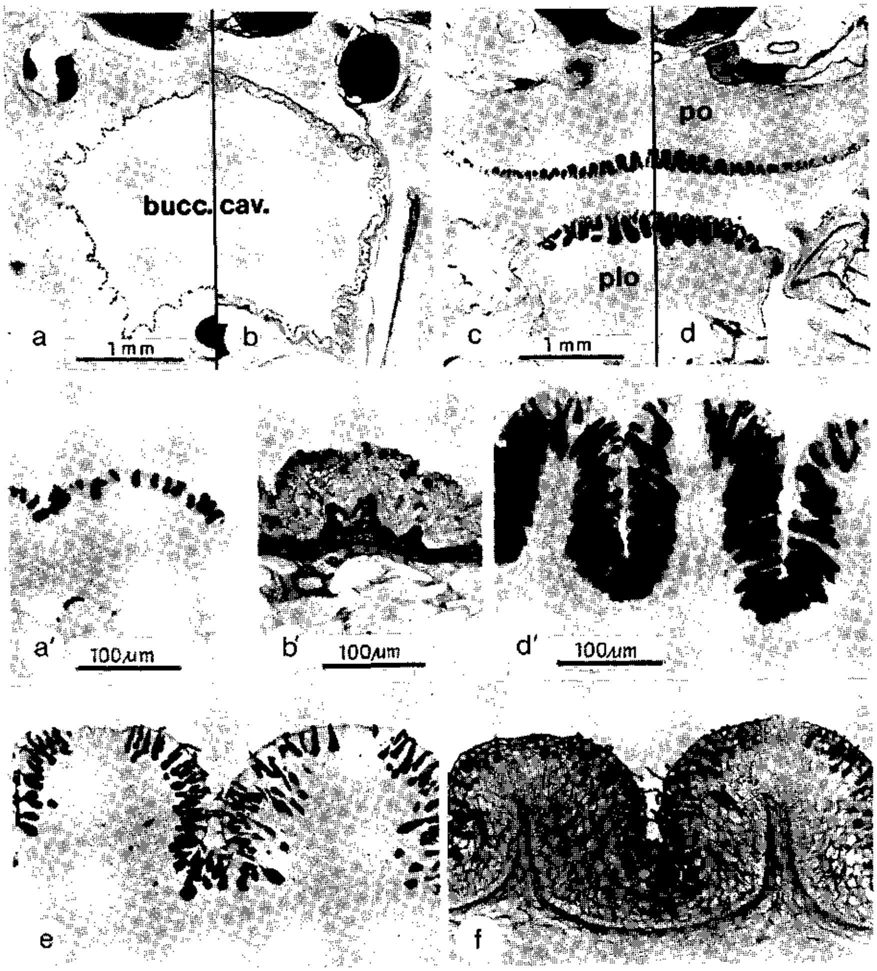

PLATE VII. **(ab)** Successive cross sections through the buccal cavity. **(cd)** Successive cross sections through the pharyngeal cavity in front of the chewing pad.

AB-staining at pH 2.5 **(a, c)** shows all acid mucus, sialomucines as well as sulfomucines, present. HID-staining **(bd)** only shows the acid sulfomucines. The almost absence of sulfomucines in **(b)** and the nearly only presence of sulfomucines in **(d)** is apparent. **(a')**, **(b')** and **(d')** are details of the corresponding sections.

(ef) Mucus in the central part of the palatal organ **(e)** contains a decreasing proportion of sialomucines (light) whereas the volume of sulfomucines (dark) has increased **(f)**. Abbreviations on page 122.

mucous cells; the individual vesicles of mucus are distinct. Other probably secretory cells occur scarcely in the opercular lining of the carp (Plate VIg). No reports on such cells have been found and its underlying structure is not known.

The striking differences in size, shape and position of mucous cells in the epithelium makes a distinction between superficial small and elongated pyriform cells (Plate IVab), large sacciform cells (Plates IVc, Vd) and typical goblet-shaped mucous cells helpfull (cf. Al-Hussaini, 1945). These are characterized in Figure 2.

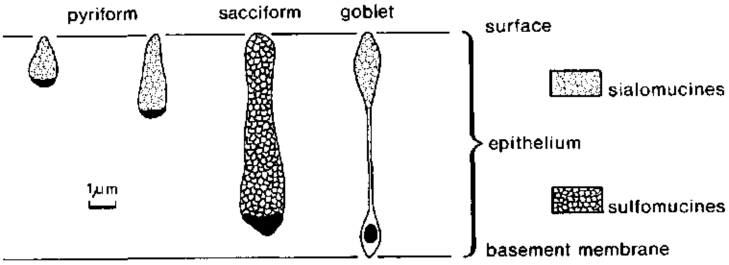

FIG. 2. Approximate shape and size of three types of cells producing mucus as they appear in the microscopic slides of the alimentary tract in the carp. Note that the sacciform cells produce sulfomucines.

Comparing the results of PAS and AB (alcian blue at pH 2.5) staining reveals that all these mucous cells secrete acid mucus. The sacciform mucous cells are all heavily stained with HID (Plate VIId, d') and thus contain sulfomucines. Pyriform cells lining the orobuccal as well as the pharyngeal lumen appear to contain much sialomucines as they are almost HID negative (Plate VIIb). The same applies to the intestinal goblet cells.

The sacciform mucous cells are distinct from other sacciform glandular cells in fish epidermis with a homogeneous mainly proteinaceous content (Mittal et al., 1981).

Club cells

The club cell is another type of unicellular gland. These large cells (ca. 18 µm diameter) always occur in the mid layers of the epidermis of many teleosts' external skin (Whitear and Mittal, 1983). They are absent in the crypts and on top of the folds. They produce a mainly proteinaceous substance in Ostariophysi (Pfeiffer, 1971) which elicits the 'fright reaction' (v. Frisch, 1941). In the carp they do not stain with PAS. They have a conspicuous centrally located nucleus in a clear cytoplasm (Plate IVa). In the carp they are not only frequent in the skin, but they also abound in the oro-buccal lining. They have not been mentioned here by Curry (1939) and Al-Hussaini (1949).

Sensory specializations

Free nerve endings, chemoreceptive single cells, taste buds, lateral line organs and free neuromasts have been found in the epithelium of fish (Fox, Lane et al., 1978). Small 'round cells', in the opercular valve epithelium of *Phoxinus* and *Ictalurus* (Whitear, 1971) resemble the possibly mechanoreceptive Merkel cells of tetrapod vertebrates (Lane and Whitear, 1977).

Villous cells

In the buccal roof and opercular lining of the carp small groups (2-6) of short microvilli (diameter 0,17 - 0,23 µm) protrude between adjacent epithelial cells (Plate VIcdeg). They closely resemble the villi of rodlet cells with speculated receptive or osmoregulatory function (cf. Karlsson, 1983). In front of the chewing pad larger fields of longer villi occur, distinct from taste buds (Plate VIf). These villi might well be part of oligovillous chemosensory cells (cf. Whitear, 1971; Whitear et al., 1983). An ultrastructural study of these villous cells should further elucidate their identity.

Taste buds

The structure, origin, development and location of taste buds is reviewed by Kapoor, Evans and Pevzner (1975) and updated by Reutter (1982). Taste buds are pear-shaped organs extending from the basal membrane to the free surface of the epithelium. Light and dark sensory cells run through their length and taper towards the free apical end into a pore (Plate Va). An intragemmal nerve plexus provides contact between the disc-shaped basal cell and the sensory cells. The lightly coloured receptor cells bear one or two long apical processes (diameter in the carp ca. 0.4 µm), the dark cells have a larger number of small microvilli (diameter ca. 0.17 µm) (Plate VIab). Only recently the demonstration of synaptic connections (Reutter, 1982) proved that also the dark cells are sensory instead of supporting as was previously assumed (Hirata, 1966).

Taste buds in the carp measure 32.5 ± 5.1 µm (width) and 44.0 ± 7.5 µm (height) averaged over all the oro-pharyngeal lining (n=60). In a second 58 mm fish the width of taste buds measured 34.5 ± 5.3 µm and the height 47.1 ± 10.4 µm (n=80). These values lie within the range reported by Iwai (1964) and Hirata (1966) for the carp. Taste buds increase in height with increasing height of the epithelium, their width appears more constant and has been used in calculating their density. The exposed receptor area of the taste bud measures 6.9-11.5 µm in diameter and generally protrudes between mostly four epithelial cells (Plate VIa). In life the mucous cuticle that covers the receptor area will only be penetrated by the large villi (Reutter, 1980).

Quantitative distribution patterns of taste buds, mucus, club cells and muscle fibers.

The distribution of these elements over the oro-pharynx is presented graphically in Figs. 3-6 and reconstructed in Figure 7.

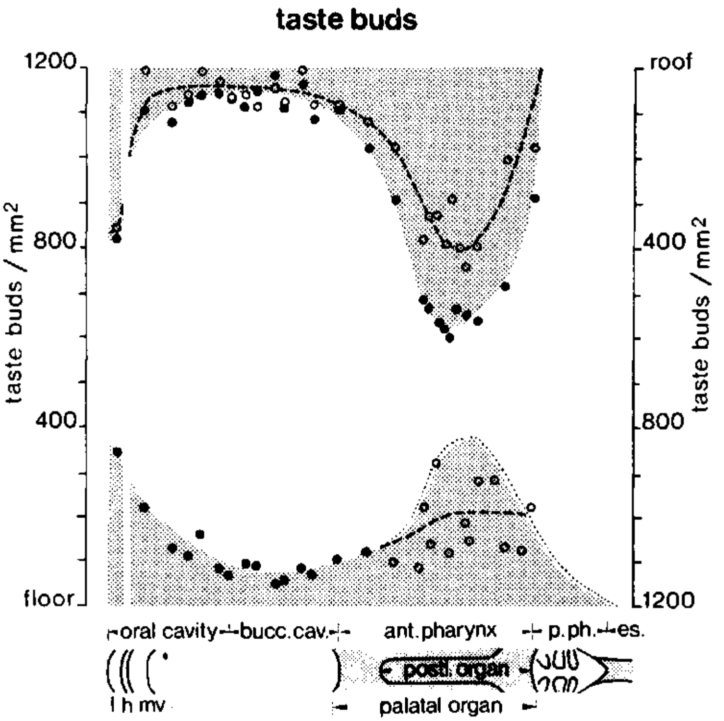

FIG. 3. Distribution of taste buds over the roof and floor of the oro-pharynx of a carp. (●) indicates averaged numbers over whole cross sections. (○) gives counts in the medial strip (cf Fig. 1), depicted as a pecked line. The dotted line indicates the part of the graph which is based on estimations from SEM-pictures and cross sections. The corresponding parts of the oro-pharynx are indicated at the bottom.
l lips, h horny area, mv maxillary valve, pph posterior pharynx, es esophagus.

Taste buds

In fishes taste buds also occur on the general body surface (Herrick, 1904; Moore, 1950; Sato, 1977; Atema, 1971). In the carp their number sharply decreases within short distance from the lips, except on the barbels.

The density of taste buds over the oro-pharyngeal surface, averaged over whole transverse sections shows two maxima in roof as well as in floor (Figs. 3,7). A narrow peak occurs in the oral area (ca. 370/mm^2) and a wider peak coincides with the palatal organ and the gill rakers, with the highest mean density of taste buds in the widest, central third of the palatal organ (ca. 580/mm^2). Due to extensive and complex folding of floor and walls in the posterior pharynx the density of its taste buds can not be measured accurately, but crude analysis shows that they have a decreasing low density, comparable to that in the buccal cavity (50-80/mm^2). No taste buds have been observed posterior to the entrance of the esophagus.

Also a conspicuous transverse gradient exists in the posterior part of the palatal organ (Fig. 6) with the highest densities (ca. 820/mm^2) of smaller taste buds (ca. 29 µm width) at the sides and lowest densities (ca. 200/mm^2) of larger width (ca. 35 µm) in the median. Comparison of the mean densities in the medial third and the total area (Fig. 3), shows that this gradient arises in the anterior part of the pharyngeal roof as well as in its floor.

In the pharyngeal floor taste buds are, as estimated from SEM-photographs, densily packed on the gill rakers (ca. 325-625/mm^2), especially at their free tops. They are less numerous on the pharyngeal surface of the arches (ca. 140/mm^2), contrary to Iwai (1964). Densities in the postlingual organ measure between 120-290/mm^2.

Mucous cells

The distribution of the relative volume of mucus over the medial oro-pharyngeal surface, irrespective of the number or type of mucous cells (see material and methods), is plotted in Figure 4. The orobuccal surface, only containing pyriform cells has a small amount of mucus, mainly sialomucines. Hardly or no mucus is found on the maxillary valve and lips.

In the pharyngeal roof two peaks are present, a small one of exclusively pyriform cells containing sialomucines in the anterior and widest half of the palatal organ, and an extremely high peak by addition of large and numerous sacciform cells, containing sulfomucines, in front of the chewing pad (Figs. 4,7).

In the pharyngeal floor a similar medial distribution pattern is present, the two peaks however partly overlap. At the rostral border of the postlingual organ the volume of sulfomucines from sacciform cells gradually increases to a high peak. Highest volumes of sacciform mucous cells are found in the posterior pharynx and most of the esophagus. As the chewing cavity merges into the esophagus pyriform cells increase and tend to equalize the decreasing sacciform cells. Both types suddenly disappear in favour of few goblet cells, typical for the intestine, close to the pyloric sphincter.

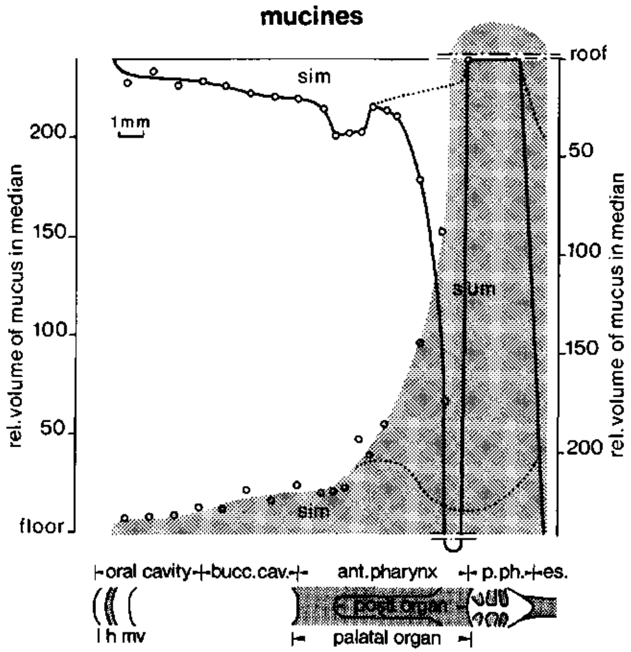

FIG. 4. Distribution of mucines over roof and floor (shaded) of the oro-pharynx, measured in the medial 300 µm strip (cf Fig. 1). The dotted line separates relative volumes of sialomucines (sim) from sulfomucines (sum) as estimated from sections with different staining (cf Plate VII).

A transverse picture in front of the chewing pad shows a small amount of pyriform cells laterally and increasing quantities of sacciform mucous cells towards the median (Fig. 6). The distribution in the pharyngeal lining covering the gill arches and postlingual organ closely parallels that in the palatal organ. Measurements in the second carp gave an identical distribution pattern with the same level of mucus.

Club cells

Though club cells have never been related to feeding, their presence in the orobuccal cavity is conspicuous. Determination of their distribution pattern may point to their role in the headgut. Club cells merely occur deep in the orobuccal lining (Plate IVa; Fig. 5). They attain densities which locally approach those in the external skin. The distribution of club cells in orobuccal roof and floor is inverse

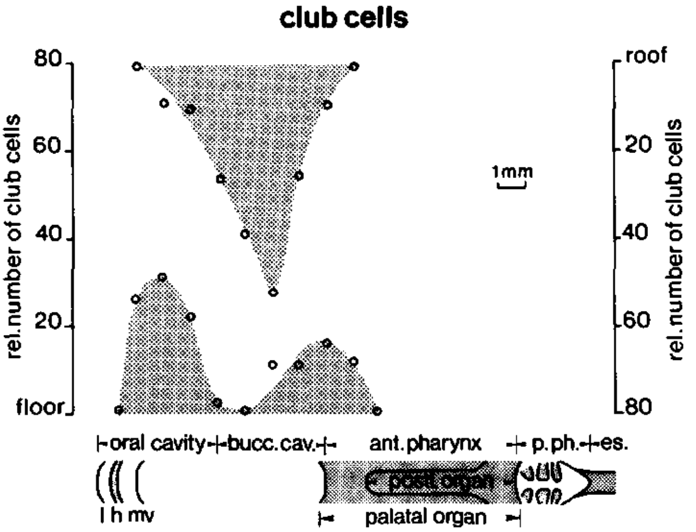

FIG. 5. Distribution of club cells over roof and floor of the oro-pharynx. Counts indicate number of inner-sections (*with cell-nucleus) in the total areas (cf Fig. 1).*

for the most part (cf. Figs. 5,7). The orobuccal roof has a high peak of club cells in its central part, whereas the orobuccal floor shows two smaller peaks in the most anterior and posterior zone. Measurements on a second carp of same origin and length gave a similar distribution pattern, but the absolute level of club cells was only half.

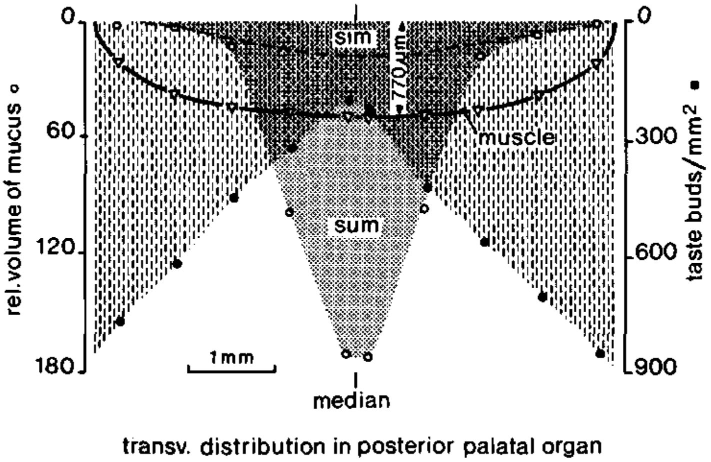

FIG. 6. Transverse distribution of taste buds, mucines and the thickness of the muscle layer in the palatal organ just anterior to the chewing pad (cf Fig. 1). Dotted line separates estimated volumes of sialomucines (small area) from sulfomucines (large area).

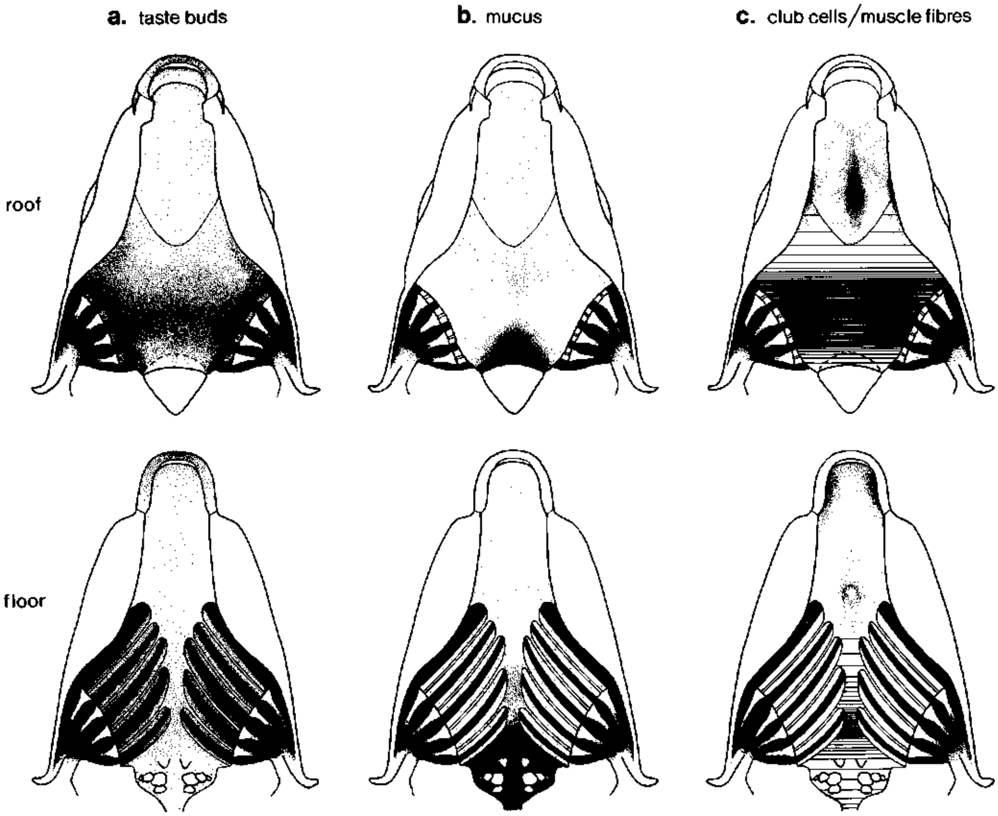

FIG. 7. Distribution patterns in oro-pharyngeal roof and floor of (a) taste buds (b) mucus and (c) club cells and muslce fibers. These drawings show the densities as depicted in Figures 3-6. Sulfomucines occur exclusively at areas with abundant mucus and cause those high densities. The low level of mucus corresponds to the presence of sialomucines.

Muscle fibers

The thickness of the shrinked muscular layers in the median is readily observed from Plate IId and measures up to 850 µm in such a small carp. It is only slightly thinner in the lateral area of the palatal organ (Fig. 6). In the postlingual organ the muscular layer only gradually increases towards the chewing cavity, contrary to the palatal organ. The gill arches at both sides of the postlingual organ have a thin muscular layer (cf. Plate IIb)
The density of muscle fibers contained in these layers increases posteriorly (cf. Plate IId) and renders thickness a rough measure. The complex structure of the wall of the posterior pharynx prevented measurement of its muscular content. This part is only roughly indicated in Fig. 7.

The distribution pattern of taste buds, mucous cells, muscle fibers and club cells allows a distinction of the oro-pharyngeal wall in six zones (Fig. 9; Table 1), each characterized by a specific combination of specialized features.
Their relation with the separate feeding actions which compose food handling and food processing in the carp are discussed later.

DISCUSSION

The role of mucus, microridges, club cells and sensory elements in the oro-pharynx

Mucus

The chemical properties of mucus were reviewed by Hunt (1970). Two main components are distinct, glycoproteins and mucopolysaccharides, organized into an entangled network. *Glycoproteins* are complexes of proteins covalently linked with varied low molecular weight saccharides. Protein properties are dominant. Sialic acid is a characteristic saccharid. *Mucopolysaccharides* are similar conjugates. Except chitine and few other structural compounds they are characterized by highly charged, high molecular weight polysaccharides of less varied nature. Polysaccharide properties dominate those of the proteins. Sialic acid is lacking, whereas sulpho-groups abound. Mucus may comprise still other components (e.g. elastine). Also do glycoproteins and mucopolysaccharides occur in other, mainly supporting, tissues (cf. Plate VIIb,d). Mucus with mainly glycoproteins are referred to as *sialomucines*, mucus with mainly mucopolysaccharides as *sulfomucines*.

Physically, mucus is a weak and reversible gel (Denny and Gosline, 1980; Silberberg and Meyer, 1982), best characterized by its viscosity and elasticity. Though sialic acid makes sialomucines rather viscous (Hunt, 1970), the highly acid sulfomucines confer mucus a high viscosity (Hunt, 1973). The carbohydrate component largely determines the rheological properties of mucus. Denny and Gosline (1980) demonstrated that large strains reduce the viscosity of pedal mucus in gastropods. The mucus recovered its solidity if allowed to heal for some period.

Mucus may perform a multitude of roles in a wide array of biological systems (Whitear, 1970; Mittal & Banerjee, 1980; Cook & Shirbate, 1983) e.g. 1) forming a mechanical barrier to foreign bodies and pathogens (it has no antibiotic effect in the carp (Hattingh and van Warmelo, 1975)); 2) forming a chemical barrier supporting osmoregulation and preventing flux of material over steep chemical or electrical gradients; 3) reducing of friction; 4) providing a mechanical buffer which protects the epithelium from damage and abrasion; 5) aiding in precipitation of suspended mud by entrapment and cleaning of the epithelium (often by cilia); 6) sticking together particulate food; 7) preventing of desiccation by binding of water; 8) enhancing adhesion in sluggish locomotion; 9) serving means of communication and navigation (e.g. molluscs); 10) feeding and attachment of young; 11) formation of cocoons and other envelopes for temporary shelter.

The orobuccal wall produces mainly sialomucines (cf. Fig. 4). This type of mucus is common to the respiratory and alimentary tract of vertebrates, probably serving protection and lubrication (Hunt, 1970). Besides soluble fish slimes on the outer skin effectively minimize the boundary layer and friction in swimming (Rosen and Cornford, 1971). Sialomucines may thus well aid in orobuccal water transport, especially at high suction velocities, when turbulent flow brings small amounts of mucus in solution.

Many sulfomucines are added posteriorly in the anterior pharynx (Figs. 4,7). This high-viscosity mucus is almost certainly related to the pure muscularly processing of food serving lubrication and reduction of the high mechanical stresses on the epithelium. They will also aid in recollection and aggregation of particles into boluses, during transport as well as during mastication and deglutition. Movement of the lateral tissue flaps in the chewing cavity, secreting a large volume of sulfomucines, might serve cleaning the occlusal surfaces. A background volume of low-viscosity sialomucines will primarily serve lubrication and it increases indeed in the esophagus.

As compared to sulfomucines, the sialomucines in the orobuccal cavity and anterolateral part of the pharynx are expected to have a reduced tendency to bind particles, as this area is largely concerned with selection between food and non-food particles by repeated resuspension (Sibbing et al., 1984).

An analogous combination of similar secretory cells cleans the mantle cavity from suspended dirt in snails (Hunt, 1973). Interactions between the two secretory products confers the mixture even a higher visco-elasticity and structural integrity than its component parts.

No tests have been performed yet to ascertain the physical properties and secretion kinetics of oro-pharyngeal mucus in fish. It is expected that the release of mucus is somehow regulated in accordance with the feeding activities of the fish.

Microridges

Mucus secreting epithelia in fish are commonly provided with microridges arranged in varied patterns. Their possible functions (Hawkes, 1974) are 1) a mechanical defense to trauma, 2) an increase of the surface area for absorbtion and gas exchange, 3) an aid in holding mucus to the cell surface. Sperry and Wassersug (1976) concluded microridges to guide the even spreading of mucus through their channels. Few of these physiological and mechanical functions have been investigated experimentally.

The differences in microridge pattern at areas of different mechanical stresses (cf. Plate VIa,b) suggest an additional mechanical function in the carp. On the lips, devoid of any specialized mucous cells, as well as in the area of the chewing cavity more microridges per unit of cell surface are found than elsewhere. Both on the lips and in this chewing area their principal role may be similar to that of the cornified cells in absorbing high forces and spreading them over the cell surface.

Club cells

These conspicuous cells never reach the surface of the epithelium, lack pores and do not contact blood vessels. They are supposed to be holocrine glands producing the alarm substance in ostariophysans and releasing this stored pheromone by damage (Pfeiffer, 1960). Alternative club cell functions which are suggested in the literature are antipathogenous action, vehicles for antibodies, toxic cells, mechanical protection and lubrication (Whitear and Mittal, 1983). Club cells do also occur in some non-ostariophysan teleosts (cf. Whitear, 1981) e.g. the eel where they are said to be involved in fibrous mucus production (Reid, 1894).

In the carp, club cells extend from the outer skin into the orobuccal cavity (Fig. 7). Their mid-epithelial location neither at the top of folds nor in the crypts where taste buds and mucous cells respectively abound, points to a rather indifferent role of their position. If these club cells have alarming functions they should be selectively emptied due to stimuli by harmful objects, not by those of the food to prevent false alarm. Large damage will impede the functions of the orobuccal epithelium in feeding. These arguments makes their alarming function in this area doubtful, even though club cell densities are highest at areas of most probable mechanical impact e.g. inside the lower jaw (Fig. 7). They may well serve other unknown functions, possibly released by neural or hormonal mechanisms. Their absence from the pharyngeal lining suggests a direct relation between club cells and the flow of water. Their slightly positive reaction on HID staining (Plate VIIb') indicates the presence of some sulfomucines in their cytoplasm in addition to the commonly known proteins.

Sensory structures

Mechano- and chemoreceptors are required to sense the qualities of the ingested material during the subsequent actions in food processing. Besides the fish needs constant monitoring of the quality and velocity of the water during respiration and feeding.

Mechanoreception

Apart from the lateral line system and free neuromasts (cf. Plate Icd) few evidence on mechanoreceptive organs in teleost skin is available (Fox et al., 1980). Many types of nerve plexuses in or below the epithelium are attributed mechanoreceptive functions (Grzycki, 1954; Whitear, 1971; Ono, 1979). Specialized epidermal cells resembling Merkel cells of higher vertebrates have been described (Lane and Whitear, 1977) but nothing is known of their physiology. As these cells are characterized by few apical finger-like villi, the presence of small groups of short villi in the buccal and opercular lining (Plate VI) may well suggest here mechanoreception in the carp.

Reutter (1974) investigated previous hypotheses (Kolmer, 1927; Hirata, 1966) that taste buds could also serve mechanoreceptive functions. He distinguished three types of taste buds in the headgut of the swordtail based on their position with respect to the surrounding epithelium. This distinction was supported by neurohistochemical characters (Reutter, 1973). Accepting Reutter's theory most protruding taste buds (type I), which would be most effective in mechanoreception, in the carp occupy the gill rakers (Plate III). Less protruding buds (type II) line the buccal folds. The other taste buds never rise above the normal level of the epithelium and their mechanoreceptive role is improbable. McGlone (1977) reports the palatal organ to respond to tactile stimuli at all stages of denervation with local bulging, possibly caused by proprioceptive reflex loops. Konishi and Zotterman (1963) found some glossopharyngeal nerve fibers in the palatal organ of the carp reacting exclusively to mechanical stimulation. Whether these fibers originate from taste buds with mechano- as well as chemoreceptive properties, or from separate mechanoreceptors is unclear. Processes like the adjusting of force, direction and amplitude of masticatory movements to the mechanical properties and momentaneous size of the food as well as decisions whether the main fraction of particles is suited for deglutition, require detailed information and feed back regulation. It is supposed that proprioceptors in the masticatory muscles and in the tissue flaps projecting between teeth and chewing pad are the main sensors in mastication. Proprioceptors in the gills of teleosts appear to respond to displacement of the gill rakers and gill filaments (Sutterlin and Saunders, 1969). Ballintijn demonstrated that tension and length receptors in respiratory muscles play a role in steering the respiratory movements in fish (Ballintijn, 1972; Ballintijn and Bamford, 1975; Ballintijn, 1982). The few unexpected muscle fibers between the chewing pad and its bony socle may well play a sensory role.

Chemoreception

The chemoreceptive properties of taste buds are evident. They have varied sensivity spectra. Konishi and Zotterman (1963) recorded responses from the glossopharyngeal nerve fibers in the carp and subdivided them into seven groups according to their response on a wide array of sapid solutions including human saliva, enabling the fish a high level of gustatory discrimination. Some appeared to have a wide gustatory spectrum, others a narrow one.

The important role of such sensors in a bottom feeder like the carp is evident, but their distribution pattern remains to be explained. In fact a density of 820 taste buds/mm^2, as found in the lateral part of the palatal organ, has not been reported previously. Given the mean width of a taste bud, about 1200/mm^2 is the maximal number (cf. Plate Va). Iwai (1964) reports a maximum of 285/mm^2 on the branchial arches of the cyprinid *Biwa zezera*.

Besides taste buds the peculiar villous cells in the oro-pharyngeal lining of the carp (Plate VI) might be involved in chemoreception.

The pharyngeal wall and its mechanisms for selection between food and non-food

Details of the way the perpendicular crossing muscle fiber systems (cf. Plates IVb, Vc; Fig. 8) react on stimuli to fix food particles at particular spots, at the same time allowing the flushing away of non-food particles, are unknown. The present and previous studies have accumulated important indirect evidence for such a role of the palatal organ.

Present data show an enormous density of taste buds up to maximal values in view of their size. It is hard to conceive that such a sensor density is not paralleled by a comparably detailed output processing of the effector system. Analysis of gut contents of carps demonstrates that few unedible material is present (Wunder, 1936; Uribe Zamora, 1975), so the system selecting between food and non-food works. Local electrical or tactile stimulation of the palatal organ results in local outbulging of its wall. Carps of 20-30 cm can handle effectively particles of about 500 µm in diameter (Uribe-Zamora, 1975). Based on these as well as the present structural details it seems justified to formulate some hypotheses as to the actual mechanism that effects selective retention of particles.

Three levels of movements of the palatal organ are suggested, related to size differences in particles offered to the system.

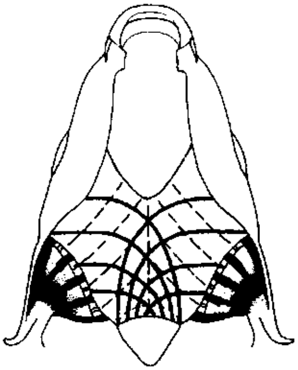

FIG. 8. Main directions of muscle fiber systems in the palatal organ are indicated by solid lines. Pecked lines show main muscle fiber directions in the pharyngeal floor. Perpendicular to these lines another not depicted fiber system is present in palatal and postlingual organ.

a) *Movements of the palatal organ as a whole*

The palatal organ lies closely to the series of four paired epibranchials and three paired pharyngobranchials belonging to the four gill bearing arches. These are suspended from the braincase by series of external and internal levator muscles as well as interconnected by oblique muscles. During respiration part of these dorsal gill arch muscles are active (Ballintijn et al., 1984). The combined activity of the gill arch muscles will be able to expand, depress and lift the palatal organ as a whole or locally. The expected palatal movements will be minute in amplitude. Slight antero-ventral movements seem possible. Through these movements large areas of the palatal organ could be closely approached to parts of the branchial basket with its numerous gill rakers. This hypothesis will be verified by electrical stimulations of the involved muscles and by electromyography.

b) *Local movements in the palatal organ, areas of several square mm.*

Such local bulgings of the palatal organ do occur (Jara, 1957; McGlone, 1978). Simultaneous contractions in the posterior area of the palatal and postlingual organ even propel the food by peristalsis-like movements in transport (Sibbing et al., 1984). Contraction of the grid of muscle fibers in a particular area will exert compression on the local interstitial fluid and so cause bulging of the epithelium into the pharyngeal slit. Whether or not the papillae are involved, is not known. The differences in main directions of the muscle fibers in pharyngeal floor and roof, except in the posterior transport area (Fig. 8), might even lead to the local production of ridges which cross at roughly 45° angles in roof and floor. Here particles could be fixed. This hypothesis assumes equal contractions of the perpendicular crossing muscle fibers for bulging and unequal contractions for ridging.

c) *Minute local movements of areas below one square mm.*

Especially anteriorly the palatal folds form papillae with a conspicuous muscular core. In areas with an increased pressure on the interstitial fluid the local effect of the pressure on shape and size of these minute projections depends upon the activity of the muscle fibres in their core and on the arrangement of the connective tissue fibers below the papillar epithelium. In these circumstances fluid pressure and muscle fibre force act antagonistically and can so determine shape and size of projections. The size of such papillae varies from ca. 150 x 550 μm anteriorly to a circular form with a 90 μm diameter more laterally. Posteriorly, at the lateral edges of the palatal organ and branchial sieve, papillae are virtually absent and the connective tissue coat vanishes (Plate Va).

The latter hypotheses can be tested with small canulae and pressure transducers combined with photographic data. The muscles of the branchial basket, the muscular strips over the gill arches, the muscular pads on the gill rakers and their movable connection with the gill arches may all contribute or even solely be responsible for local retention of particles. The papillae can also be explained as a surface increase for mucus supply. The huge vagal lobes and their complex cyto-architecture (see below) seem to be in accordance with the detailed movements suggested above. The bottom feeding habits of carps have profound influences on structures and functions in the oro-pharynx.

Pathways connecting oro-pharyngeal sensors and effectors

To obtain a more complete picture of food processing some important facts from the literature on this subject have been compiled in the following lines.

Peripheral pathways

Herrick (1899, 1901, 1906) concluded from his extensive studies on the senses of touch and taste in fishes that the nervus trigeminus (V) is the main pathway for touch impulses from the orobuccal skin, whereas the facial nerve (VII) mainly carries the sensory input from taste buds from the same area. The posterior buccal taste buds send their information through the glossopharyngeal nerve (IX), the pharyngeal taste buds through the large vagal nerve (X). Nerves VII, IX and X project on distinct regions in the brain, respectively the facial, glossopharyngeal and the vagal lobes. Little detailed knowledge exists on the origin and termination of their motor components.

Evans (1952) suggested that feeding behaviour is expressed in the morphology of the brain. When taste buds abound on the external skin, barbels and lips such as in skin tasters like catfishes and minnows, the facial lobe is conspicuous. In mouth tasters such as the carp and goldfish the vagal lobe is greatly enlarged. Sightfeeders have large mesencephalic optic lobes. Evidence now exists from the catfish that the facial gustatory system is involved in locating and sensing an external food source while the vagal gustatory system determines the palatability of the food (Atema, 1971)

Contrary to the facial lobe, the vagal lobe in cyprinids has a highly organized laminar structure (Herrick, 1906; Ozawa, 1951; Ito, 1971). The ascending projections were found to be topographically arranged (Morita et al., 1983). McGlone's physiological studies on the goldfish suggest some degree of somatotopy with respect to the palatal organ. Application of the horseradish peroxidase technique (Luiten, 1975b) by Finger (1981b) labeled only restricted small areas in the palatal organ and in the vagal lobe, supporting the palatotopic mapping in the vagal lobe. This suggests a gustatory reflex mechanism regulating local palatal muscular contractions. As the palatal organ performs its functions in close coordination with the postlingual organ in the carp (Sibbing et al., 1984) we hypothesize that the postlingual organ is similarly mapped in the vagal lobe.

Generally the pharyngeal taste buds of teleosts are innervated according to the following pattern. The glossopharyngeal nerve (IX), after supplying the anterior branchial levator muscles, sends a ramus into the most anterior part of the palatal organ. More ventrally it divides into a sensory pretrematic branch to the hyoid area and a posttrematic branch to the first hemibranch, supplying mucous epithelium, taste buds, gill rakers and the gill arch musculature. This suggest that opposed areas of the pharyngeal roof and floor are locally innervated by the same branch. In a similar way four rami of the huge vagal nerve (X) innervate corresponding areas around each of the subsequent four gill slits. Posterior vagal rami innervate the sensory and effector components of the pharyngeal masticatory apparatus and one runs caudad into the esophageal wall.

The scattered chemosensory single cells in the buccal and opercular lining may well belong to the general cutaneous chemosensory component (Whitear, 1971). No evidence exists on their innervation and specific role. The common chemical sense in the skin generally detects the qualities of the water (avoiding reactions) and is only exceptionally (e.g. in Triglids) used in food-seeking (Scharrer, 1963).

Central pathways

Steering the whole concert of movements in food uptake, selection, transport, mastication and deglutition for efficient food processing as a whole, tuned to the type of food (Sibbing et al., 1984) requires integration of enormous sensory inputs on a higher level in the brain. Distinct central connections exist between projections of nerves V, VII, IX and X in the carp (Luiten, 1975a). These areas process not only taste information but also signals from other sources e.g. touch, proprioception from the gills and jaw muscles. The central gustatory paths in the closely allied crucian carp (*Carassius carassius*) (Morita et al., 1980) also suggest complex integration mechanisms between sensory input and motor output regulating cyprinid feeding.

Six specialized areas in the oro-pharynx related to food handling in the carp

This summarizing section relates distinct areas in the oro-pharynx which are characterized by a particular combination of structural specializations (Figs. 9; Table 1) to their sensory and effector roles in feeding. The mechanisms and stereotyped movements of twelve distinct actions composing a feeding sequence have been discussed previously (Sibbing, 1982; Sibbing et al., 1984). These actions are particulate feeding and gulping for food intake; rinsing, repositioning, back-washing and spitting for food selection; recollection of food from the branchial sieve, transport and loading; crushing and grinding; deglutition.

In this paragraph the structures of young fish (5.8 cm SL) are related to the feeding mechanisms of adult fish (ca. 30 cm SL). It is well known that the feeding habits and mechanisms of fish larvae differ from the adult fish (Stroband and Dabrowski, 1980). So could do their structures associated with feeding. Campos (1969) calculated that during the development of *Phoxinus* larvae taste buds in the pharynx are increased in number firstly, those in the buccal cavity follow later. The adult distribution pattern is established at 10 mm length of the larvae. A review on the feeding habits on larval and adult carps (Uribe-Zamora, 1975) shows that dietary changes occur in the early larval stages mainly (the first three weeks after hatching) and that carps of the two size classes already have similar feeding habits. No conspicuous differences have been found in the oro-pharyngeal wall in a comparison with a larger carp (20 cm SL).

DISTINCT AREAS IN THE ORO-PHARYNGEAL WALL AND THEIR ROLE IN FOOD HANDLING

	taste buds per mm^2	mucines		muscle layers	club cells	cornification	str.comp. fibr.layer	expanded shape	role in food processing
		sialo	sulfo						
A. lips	370	-	-	-	-	+	37 µm		detection manipulation
B. orobuccal cavity	60	+	-	-	+	-	26 µm	cone	suction and resuspension chamber
C. ant.zone ant.pharynx	100→520	++	-	+	-	-	12 µm	coarse slit	coarse selection of large particles
D. lat. area ant.pharynx	580	+	-	++	-	-	2 µm	fine slit	selection of fine particles
E. post. zone ant.pharynx	570→200	+	++++	+++	-	-	5 µm	appressed	aggregation transport loading teeth
F. posterior pharynx	200→0	+	+++++	+	-	+++	1 µm	bulb	mastication deglutition

TABLE 1. Distinct areas in the oro-pharyngeal wall characterized by a specific combination of specializations, as depicted in Figs. 7, 8. The role of these areas in food processing is indicated (Sibbing et al. 1984). Further explanation in text.

Detection and oral manipulation (area A)

The taste buds on barbels and lips (380/mm^2) are the primary sensors detecting food at bottom feeding. They repetitively contact and scan the substrate at probing. Taste information is passed through the facial nerve (VII) to its large lobe in the brain. Free neuromasts possibly aid in detection of moving food objects. No mechanoreceptors for recording the velocity of flow or for touch could be recognized. Though carps are primarily night and bottomfeeders additional visual cues alarm and guide the fish to pelagic and surface dwelling prey at daytime.

Pressures on the lips will be considerable and taste buds lay sunken in a thick epithelium with dense microridges and without mucous cells, backed by a firm coat of collagen. At the contact area of the jaws the epithelium is cornified and devoid of taste buds, resisting abrasion during manipulation of gravel, bottom substrate and macrophytes.

Ventrad protrusibility of the upper jaws allows the fish to exploit the bottom substrate in depth while it at the same time can extend its search area by swimming with an oblique angle of the body axis. Soiled food is taken, requiring internal selection between food and non-food particles. As the protruded mouth is small and cylindrical a high and directed suction force can be achieved to increase the water velocity for ingestion of large (up to 9% of its bodylength), heavy, deeply hidden or otherwise less accessible particles. The small suction area and the type of swimming almost excludes capture of large and rapid prey. The lack of oral teeth excludes biting large objects (e.g. macrophytes). The direction of protrusion is readily adapted to the specific location of the prey. Proprioceptors within the jaw muscles are known to assist in steering the jaw movements.

Flow and resuspension of water and particles (area B)

Expansion of the orobuccal cavity occurs during food uptake. Unfolding by protrusion enlarges the anterior part of the oral cavity considerably. Suction of particles is however mainly caused by voluminous opercular expansion, pharyngeal widening plays a minor role. The posterior part of the buccal cavity gradually widens and flattens, thus spreading and retarding the flow and retaining large objects from the water to be expelled. Pyriform mucous cells produce low-viscosity sialomucines for physiological and mechanical protection, and effect a considerable reduction of friction at large velocities of suction by maintaining a laminar flow along the buccal wall. Widely spaced microridges on its surface may assist in holding the mucus. The orobuccal cavity furthermore functions as a chamber for gustation and resuspension of particles in selection. Particles are washed back- and forward by closed protrusion movements and compression. Highly viscous sulfomucines that would aggregate small particles are conspicuously absent in this area. Oligovillous cells and taste buds in the buccal lining, though of low density (50 tb/mm^2), are probably more important in scanning the flow of water and particles during resuspension, than at particulate intake. At particulate intake this cavity is rapidly passed by food items. Club cells appear related to the flow of water because they occur almost exclusively in the oro-buccal lining. Their position in the oro-buccal epithelium and the supposed release of their contents by damage renders their alarming function in this area doubtful. No definite mechanoreceptors monitoring the flow have been found, but the slightly protruding taste buds or the oligovillous cells may have some mechanoreceptive functions.

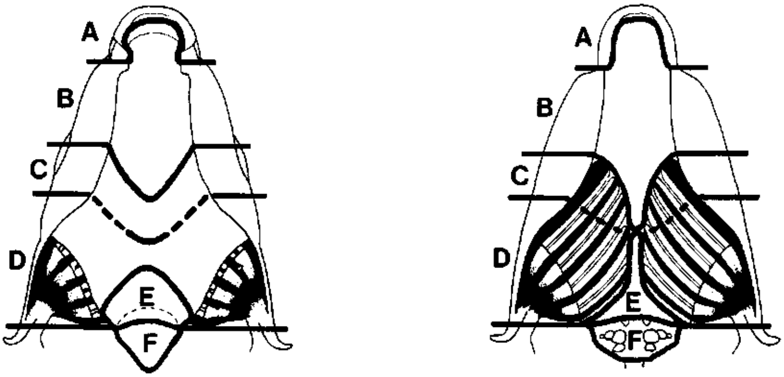

FIG. 9. Areas in oro-pharyngeal roof and floor, characterized by a specific combination of morphological characters and employed in the separate actions which together compose feeding sequences (cf Table 1.). Pecked lines indicate less sharply demarcated areas.

Coarse selection of large particles (area C)

The presence of a thick muscular lining in the pharynx, and its absence from the orobuccal cavity evidently reflects the different mechanisms of particle transport viz. by flow or by muscular bulging. The conspicuously different profiles of the orobuccal cavity, cylindrical, and the pharyngeal cavity, narrow and slit-like, are adjusted to these different mechanisms. The most anterior part of the pharynx (area C in Fig. 9) traps large particles between roof and floor. The average taste bud density increases sharply from 100 to 520 per mm^2 providing the sensory information required for decisions how further processing should occur. The increased amount of sialomucines in the epithelial crypts facilitates handling of particles.

Water and small particles are further spread between palatal organ and branchial sieve. This area is controled by the glossopharyngeal nerve IX and the anterior rami of the vagus (X).

Selection of small particles (area D)

At bottom feeding food must be selected from non-food. The optimization of the ability to use tiny dispersed food particles present among non-food particles is decisive in the exploitation of this habitat. Repetitive back-washing movements resuspend ingested particles and suggest a graded purification in the pharynx (Sibbing et al., 1984). The lateral areas in the anterior pharynx are almost maximally packed with taste buds (up to $820/mm^2$) and indicate a high resolving power in the gustatory system. Local bulging of the palatal organ, possibly combined with activity of the movable gill rakers and their muscular pads, most probably clamp food particles between roof and floor, while waste is drained with the water. Few pyriform mucous cells (sialomucines with low viscosity) will aid in particle handling. Locally varied activity in the palatal organ has been recorded (Sibbing et al., 1984) and the palatal bulging can readily be stimulated. The arrangement of fibers in the pharyngeal roof and floor as well as the interspersed connective tissue and fluid might well allow quite local fixation of particles. Taste information is carried to vagal lobes of enormous size. Their laminated organization suggest a palatotopic mapping of the pharyngeal wall. The muscular papillae covering the anterior surface of the palatal organ serve very local retention of particles or merely increase the sialomucines supply. They are larger in the area for trapping and selection of large particles (area C).

The protruding position of taste buds on the gill rakers might confer them mechanoreceptive functions. The importance of flow regulation during size-selection, cleaning of the branchial sieve and recollection of food particles for transport seems without doubt. The papillae provide the gill rakers with profiles most probably affecting the mesh-width of the branchial sieve in selection between size-classes of food particles. Proprioceptors are known to occur in gill filaments and rakers. The slit-like profile of the anterior pharynx is a structural necessity for the present selection process and is probably influenced by palatal movements as a whole and assures a large contact area. Large food objects can not pass.

Transport of food and loading of the chewing cavity (area E).

The triangular postlingual area in front of the chewing cavity is excluded from the lateral paths of flow. The massive muscular roof and floor fill the pharyngeal slit. The arrangement of the muscle fibers and the activities in this area, coordinated in roof and floor, take care of food transport (Sibbing et al., 1984) and its propulsion into the chewing cavity. They also prevent loss of food from the chewing cavity during mastication and deglutition. High longitudinal folds direct the movement of the food, lubricated by a copious mucus supply. This mucus is largely composed of highly viscous sulfomucines, which now also will aid in aggregation of food particles sticking together into boluses for further transport. Though taste buds are still numerous (ca. 200/mm^2) their density as well as the muscular content of the folds is less than in the anterior areas (C, D). Taste buds do not protrude from the epithelium. Mechanoreceptors steering transport have not been recognized.

Mastication and deglutition (area F)

Movement of the pharyngeal teeth with respect to the cornified chewing pad requires extensibility of the posterior pharyngeal wall. Particles larger than ca. 3% of the body length of the carp can not enter the chewing cavity. The composition of the epithelium is however closely similar to that of the postlingual area (E). Foliaceous papillae crowded with cells producing sulfomucines lubricate mastication and aggregate ground particles into boluses. Lateral muscular tissue flaps may clean the occlusal surfaces from particles, acting like a tongue. Muscle fibers are part of the sphincter oesophagi. This muscle supports masticatory movements and is the prime effector in deglutition, propelling the food into the esophagus (Sibbing, 1982).

Taste buds control the contents of the masticated food and their anterior density (200/mm^2) decreases sharply in the direction of transport. They vanish on the folds converging into the esophagus. Proprioceptors in the pharyngeal jaw muscles are supposed to play a prominent role in steering masticatory movements. Mechanoreceptors have not been recognized.

The complex central pathways in the posterior brain are supposed to fulfill the integration of the subsequent actions into an efficient feeding sequence, adjusted to the type of food.

The combined mechanisms for uptake, selection and mastication although specialized for bottom feeding allow also other food sources to be exploited (e.g. pelagic). Limitations on these have been outlined previously. That carps may even be considered as pests is most probably also due to the features discussed in this paper.

ABBREVIATIONS

ac	anterior cartilage	gr	gill raker	pb	pharyngobranchials
ad	aorta dorsalis	h	hart	pj	pharyngeal jaw
am	adductor mandibulae	ib	intestinal bulb	plo	postlingual organ
ap	anterior pharynx	l	lip	pm	pyriform mucous cell
at	adipose tissue	lj	lower jaw	po	palatal organ
b	barbel	ll	lateral line system	pp	posterior pharynx
bc	buccal cavity	mf	muscle fibers	pt	pharyngeal teeth
c	cornified area	mv	maxillary valve	ropi	inf. retractor phar. jaw
cc	club cell	n	free neuromast	rops	sup. retractor phar. jaw
cp	chewing pad	ob	olfactory bulb	sc	stratum compactum
ep	epithelium	oc	oral cavity	sm	sacciform mucous cell
es	esophagus	occ	occipital skull area	sth	sternohyoid muscle
f	fibrous layer	ol	olfactory organ	tb	taste bud
fl	facial lobe	op	oral papillae	tf	tissue flap
fn	facial nerve	opc	opercular cavity	uj	upper jaw
ga	gill arch	p	papillae	v	vertebrae
gf	gill filament				
gh	geniohyoid muscle				

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Pharyngeal Mastication and Food Transport in the Carp (*Cyprinus carpio* L.): A Cineradiographic and Electromyographic Study

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ABSTRACT Cyprinids constitute the largest fish family and are characterized by their pharyngeal teeth. The masticatory mechanism is still poorly understood. The complex of structures that determine the movements of pharyngeal teeth and chewing pad in the carp (*Cyprinus carpio* L.) is analyzed. Activities in 16 head muscles of a free-swimming carp were recorded. X-ray cinerecordings, synchronized with electromyograms, were made of the intake, transport, mastication, and deglutition of radiopaque food pellets. Metal markers allowed a detailed movement analysis.

Masticatory cycles are bilaterally synchronous and show distinct crushing and grinding patterns. Direct masticatory muscles that suspend and connect the pharyngeal bones steer and stabilize the masticatory movements. Baudelot's ligament, between skull and pectoral girdle, is applied as fulcrum, effects a crucial shift of the rotation axis of the pharyngeal jaw, and transforms crushing into grinding; simultaneous abduction lengthens the grinding stroke. Body muscles supply indirectly the power for mastication; they also appear to be regulated more distantly. The epaxial muscles lift the skull and thereby the levators of the pharyngeal bones, thus transmitting high forces to the teeth. They also stretch the levator of the bone as soon as occlusion is reached and thus optimize its production of forces during grinding. The hypaxial muscles retract the pharyngeal bones indirectly during grinding and power the teeth in sliding. The chewing pad, previously assumed to be motionless, rotates rostroventrad with the skull and intensifies grinding.

Respiration and mastication are mutually related. The extensive movements of the pharyngeal bones are permitted only by the simultaneous expansion of the buccopharynx and a slide-coupling in the branchial floor. Muscular pads that line the pharynx are shown to transport food toward the teeth. The constrictor pharyngis effects deglutition.

Natural food, intestinal contents, and feces of the carp were analyzed with respect to the capacity for distinct masticatory operations. During the experiments pellets, barley, and worms were fed. The carp is specialized for polyphagy and this appears to be based on the profiles of the heterodont teeth rather than on drastic changes in the two preprogrammed activity patterns. Comparison of the pharyngeal jaw system in the carp and higher teleosts emphasizes the structural design for the application of large forces in this cyprinid.

The Cyprinidae, with 275 genera and about 1,600 species, is by far the greatest family of teleost fishes, characterized, among other features, by pharyngeal teeth in one to three rows with never more than eight teeth in a single row (Nelson, '76). Pharyngeal teeth and bones are important characters in phyletic studies on cyprinids (Hensel, '70). The mechanism of mastication in carps and its bearing on other components in the head have never been fully elucidated.

The morphology of pharyngeal bones and teeth in the cyprinids is tremendously varied (Heincke, 1892; Chu, '35). Teeth are large or small, and arranged widely spread or closely together in multiple short or in single long rows. In the grasscarp (*Ctenopharyngodon*) they interdigitate from left and right sides, in the carp they do not. This variety is assumed to reflect an adaptation of cyprinid species to diversified trophic conditions.

There are scattered descriptions of the lower pharyngeal bones and teeth (Jurine, 1821; Owen, 1840–1845; Heincke, 1892; Shepherd, '12; Stoss, '21; Chu, '35; Vasnecov, '39; Rutte, '62), the horny chewing pad opposite the teeth and fixed at the posterior base of the skull (Gratzianow, 1900; Haempel, '07), and of the pharyngeal bone musculature (Haempel, '09; Takahasi, '25; Girgis, '52; Eastman, '71) of different cyprinids. For a review of literature on pharyngeal masticatory elements in the carp, the reader is referred to Eastman ('70). The studies mentioned treat only disjoined elements, are mainly comparative, and do not evaluate the whole set of masticatory elements, let alone their interrelations. Such a holistic approach is essential in explaining the >relationships between structural elements of the feeding mechanism and the ecological conditions of some African cyprinids. In addition to the pharyngeal masticatory apparatus, external features and prehensile, selective, and digestive structures were studied also. Matthes ('63) distinguishes three basic types of African cyprinids: a Labeo (microphytophagous), a Barbus (omnivorous), and a Barilius (carnivorous) type. Eastman ('70) treated the pharyngeal masticatory apparatus in the carp and in the River Redhorse (*Moxostoma carinatum*), made some comparison with other Minnesota cyprinids and catostomids, and used pharyngeal bones and teeth to establish taxonomic keys for these fishes. Until now no functional study of mastication in cyprinids has been performed and the function and interaction of the separate and varied elements, such as teeth, chewing pad, bones, muscles, and ligaments, are still unknown. The present study demonstrates that, besides these directly involved elements, skull and pectoral girdle also participate in mastication.

The aim of this study is to determine which elements of the head are involved in pharyngeal mastication, their actual role, the relevance of topography, form, and structure, and how the various actions are integrated into effective masticatory movements. Owing to the integration of a multiplicity of functional components in the head, attention should be paid to competitive demands of other than masticatory functions on the pharyngeal structures (Dullemeijer, '58, '74). The present analysis comprises form as well as action. It includes the recording of activities in the small and less accessible pharyngeal muscles in free-swimming and feeding carps (*Cyprinus carpio* L.), with simultaneous X-ray cinematography of pharyngeal bone movements.

A study of the relation between form and function of the masticatory apparatus should also involve an analysis of the natural food and a differentiation according to its shape, size, and mechanical properties. Cyprinids are highly suitable for studying the relation between mastication and diet in fishes, because the absence of any other teeth and the lack of a stomach might well increase the demands on the pharyngeal masticatory construction. The presence of a flat and fixed chewing pad in cyprinids instead of complex and movable suprapharyngeal teeth, as in most other teleosts, simplifies the mechanical events between the diminutive surfaces and facilitates the search for relations between properties of the food and the morphology of the teeth.

The common carp (*Cyprinus carpio* L.) was selected because it is readily available and withstands experimental manipulation. Its respiratory pump was studied by Ballintijn ('69 a,b); thus, there is a solid basis for evaluating the anticipated relations between mastication and respiration. Because the carp is extensively cultured, knowledge of its feeding mechanism might prove valuable for pisciculture.

The present study provides a standard of comparison to be used in future comparative studies within this family.

MATERIALS AND TECHNIQUES

Dissection and experiments were carried out with 3-year-old mirror-carps (*Cyprinus carpio* L.), standard length 28–38 cm. obtained from the OVB (Organisatie ter Verbetering van de Binnenvisserij, Utrecht, the Netherlands). Some were dissected fresh; others were fixed in formalin or Vin d'Alsace (Zweers, '74).

Prior to inserting electrodes and platinum markers, the animals were superficially anesthetized with a solution of 125 mg/liter MS 222 (Sandoz, Basel); the lower jaw kept slightly moving. Electromyograms were recorded as soon as the actively swimming fish started to feed, in most cases half a day after being returned to the experimental tank (80 × 50 × 40 cm), at about 20°C. Damage to the fish was only slight and restricted to the last gill arch;

> structure of the parts (Dullemeijer, '58) and was made by Matthes ('63) who analyzed the

within a week the injury disappeared. Nevertheless, no fish was used more than twice for experiments.

The food usually consisted of industrial trout pellets (Trouvit 4, diameter 5 mm; Trouw and Co., N.V., Putten, the Netherlands), and occasionally of worms and barley.

Electromyography

In order to measure the activity of the muscles involved in respiration, food transport and mastication in a single experiment, up to nine pairs of insulated copper wire electrodes (Povin D, 100-μm diameter; Pope, Venlo, the Netherlands) were inserted with a modified fork-tipped hypodermic needle (Osse et al., '72). The distance between the two bared electrode tips was about 4 mm in each muscle; in very small muscles the electrodes were inserted simultaneously with one needle. The electrode positions were checked in lateral and dorsoventral X-ray photographs and in later experiments even during the operation by short stimulation (square waves, 50 Hz, 2–10 V). Three experiments included bilateral measurements.

The bundle of electrode wires was pulled through a flexible rubber tube (2-mm inner diameter) that was closed at both ends with nail-polish. The tube protects the leads, largely prevents contact with water, prevents the fish from being entangled in the wires (the air-filled tube floats), and transmits the movements of the fish better to the collector. The cable was fixed to the first spine of the dorsal fin by means of a small clamping screw.

The instruments for amplification and registration, including an ink-jet recorder (Siemens; type S), are similar to those used by Osse ('69), who described details of the measuring procedure. Filters of low and high cutoff were set at 0.08 and 10 kHz; amplification varied from 10^3 to 10^4. An instrumentation tape recorder (Bell and Howell; type CPR 4010) was added. The connection between fish and apparatus was modified by applying a 14-pole miniature slip ring and brush collector (I.D.M. Electronics Ltd., Reading, England). This plug-in collector improves the transmission of the signals through its stable gold contacts, and rotates easier with the movements of the fish.

X-ray cinematography

Lateral and dorsoventral X-ray images (Siemens Gigantos X-ray apparatus; 100 kV lateral/75 kV dorsoventral, 125 mA, and 2 msec) of the moving elements of the head were intensified (Siemens 50-kV image intensifier) and recorded with an Arriflex 35-mm motion picture camera (Agfa-Gevaert Copex Pan film) at 26 frames per second. The distances between X-ray tube and fish and between the fish and the image intensifier were 195 cm (in dorsoventral projection, 135 cm) and 5 cm, respectively.

In order to penetrate water with X-rays a high X-ray tube voltage is required, but a high voltage gives low contrast between the bony elements and the water. In order to reduce the water layer around the fish as much as possible, the fish was trained to feed in a narrow, 2.5-mm perspex cuvet (32 × 9 × 27 cm), equipped with a movable curtain behind the tail. This design also keeps the head of the fish above the image intensifier and tends to maintain the fish parallel to the plane of the film. In lateral view the fish was 4 cm thick at the pectoral girdle, and the water layer (progressively replaced by tempex) 2.5 cm; in a dorsoventral view these values were 6 and 1.5 cm, respectively. The necessary use of an image intensifier limits the definition of the images. To improve contrast and to allow accurate measurements, pieces of 0.5-mm platinum wire were inserted on selected places (Figs. 8, 17b). Markers on the skull facilitated the elimination of distorted projections. X-ray movies were evaluated and the appropriate masticatory scenes selected on a Vanguard (type 16C) motion analyzer. Measurements were made in three-times enlarged individual frames, with a Leitz Makro Promar projector provided with a film-transport adaptor. With this procedure the required accuracy was obtained for measuring the minute changes in position between successive frames.

Simultaneously with X-ray cinematography, the activity of selected muscles was recorded. X-ray frames and electromyograms were synchronized by pulse trains produced at random and registered both on the film (by flashes of a diode bulb built into the camera body) and on the EMGs. Movements were analyzed of two trained carps; from the large quantity of material about 60 of the most stably projected chewing cycles of eight masticatory sequences were selected. Measurements corresponded very well for the two fishes. At least 30 EMG experiments supplied the data for the activity pattern of the muscles during mastication and respiration. The processing of movement analysis and EMG data will be discussed later, because the necessary anatomical data have not yet been provided.

RESULTS

Description of the anatomical construction

The following anatomical details are essential to understand the functional-morphological analysis of mastication. Previous descriptions (Eastman, '70, '71) do not show the elements in their positions relative to the skull, pectoral girdle, and branchial basket. Besides, some erroneously given names need correction and some pharyngeal bone muscles were omitted. Knowledge of the possible effects of single muscle contraction on the position of the pharyngeal bones is a prerequisite for understanding the recorded patterns of muscle activity. Previous studies do not mention the ligament of Baudelot, which plays a crucial role in the mechanics of mastication in the carp.

1. The bony elements (Fig. 1,2)

The nomenclature of the skull and visceral bony elements in cyprinids follows Ramaswami ('55) and Harrington ('55).

The os pharyngea or *pharyngeal bone* represents the ceratobranchial of the fifth (V) branchial arch (Fig. 1), bears the pharyngeal teeth on the medial side (Fig. 2a), and is covered dorsally by a thick mucosa (cf. Fig. 4). The posteroventral apex, the anterior angle in Chu's terminology ('35), divides the bone into an anterior limb, contributing to the floor of the pharynx and the roof of the pericardial cavity, and a posterior limb, curving dorsad around the entrance to the esophagus (cf. Fig. 5). The dorsal process of the posterior limb reaches into the subtemporal fossa of the skull. Medially, the pharyngeal bones are connected by the interpharyngeal ligaments, and these extend rostrad into a ligamentous symphysis (Fig. 6). The pharyngeal bones are joined to the branchial basket by the anterior cartilage, a large copula extending caudad from the basibranchial III (Fig. 5).

Each pharyngeal bone bears three rows of heterodont *pharyngeal teeth* (Fig. 2). The tooth formula is 1(C)-1(B)-3(A) : 3(A)-1(B)-1(C). Yang ('64) found about 11% of 260 Korean carps to have variant formulas; Eastman ('70) reported less than 6% for 380 Minnesota carps. Developing teeth, embedded in the mucosa at the base of the functional teeth, are often present (Fig. 6). They ankylose to the bony processes supporting the functional teeth after these have been shed (Geyer, '37). The same author and others (Evans and Deubler, '55; Schwartz and Dutcher, '62) discussed the sequence and frequency of their repetitive replacement.

All teeth are molariform, except the rostral (I) tooth of the medial (A) row, which has a dome-shaped smooth crown with a pointed center (Fig. 2); this crown lies lower than those of the other teeth and is covered by mucosal folds. All flat molariform crowns are characterized by caudomediad running, slightly sinuous furrows; at approximately right angles to these, abrasion scratches are observed. Teeth of larger fish have more furrows. The closely packed crowns point slightly dorsocaudad and mediad when not involved in mastication, as appears from X-ray photographs of an anesthetized carp.

The pharyngeal teeth oppose a horny *chewing pad*, firmly embedded in and supported by the basioccipital process of the skull (Figs. 1, 2b); this process continues caudad between the anterior vertebrae and the esophagus as the pharyngeal process. Following Nusbaum ('08), the basioccipital process develops from the ventral arches of the first three vertebrae,

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Abbreviations

aa, anterior angle
ac, anterior cartilage
al, anterior limb
ar, articular
bbr, basibranchial III
bocc pr, pharyngeal process of the basioccipital
brr, branchiostegal rays
cbr, ceratobranchial I-IV
chy, ceratohyal
chp, chewing pad
clthr, cleithrum
d, dental
dp, dorsal process
ebr, epibranchial
ecpt, ectopterygoid
ehy, epihyal
enpt, entopterygoid
ghy, glossohyal
hhy, hypohyal
hmd, hyomandibular
ih, interhyal
ipl, interpharyngeal ligaments
k, kinethmoid
mpt, metapterygoid
mx, maxilla
ns, neural spines vertebrae II-IV
opj, opercular joint of hyomandibular
osu, os suspensorium
pal, palatine
pmx, premaxilla
phb, pharyngeal bone
ppb, pharyngeal process of the basioccipital
pr, pleural rib
pl, posterior limb
pt, posttemporal
qu, quadrate
sc, submaxillar cartilage
scl, supracleithrum
soc, supraoccipital
sy, symphysis
sy, symplectic
tr, trabecula
uhy, urohyal
v, vertebra
A_2A_3, m. adductor mandibulae
LOP, m. levator operculi
PRH, m. protractor hyoidei
STH, m. sternohyoideus

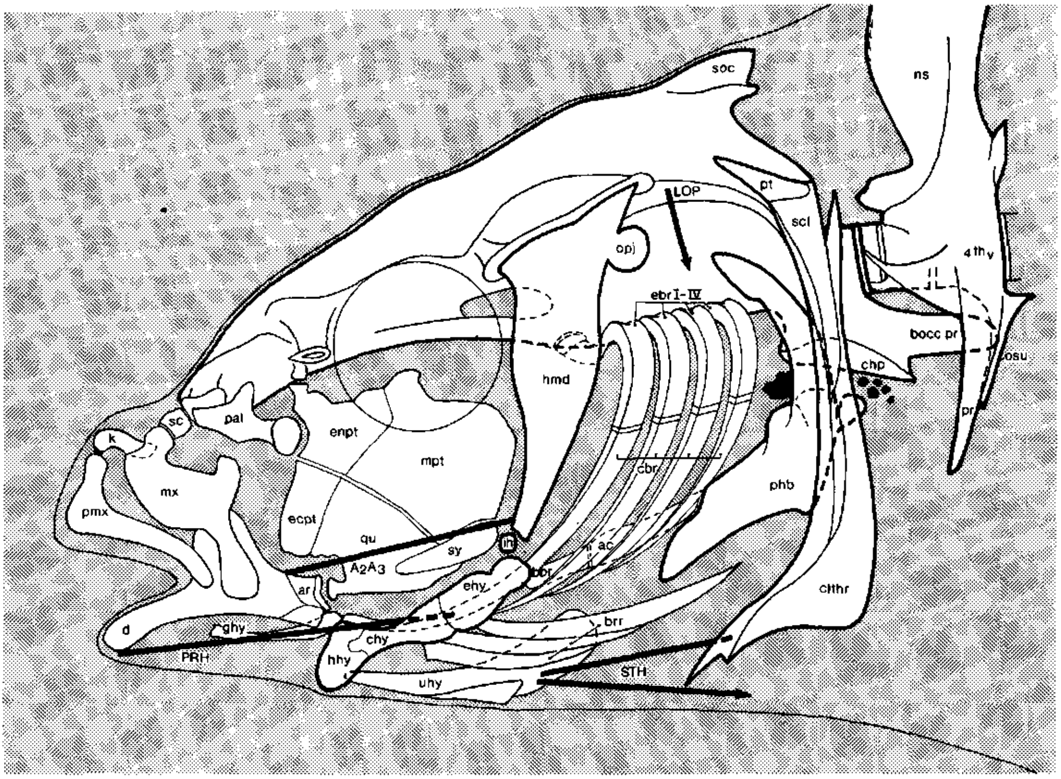


Fig. 1. Skeleton of the carp, showing the position of the pharyngeal bones and chewing pad among other components in the head (opercular and circumorbital bones removed). Only left-side elements are depicted. Heavy lines indicate muscles. Modification of Ballintijn ('69a).

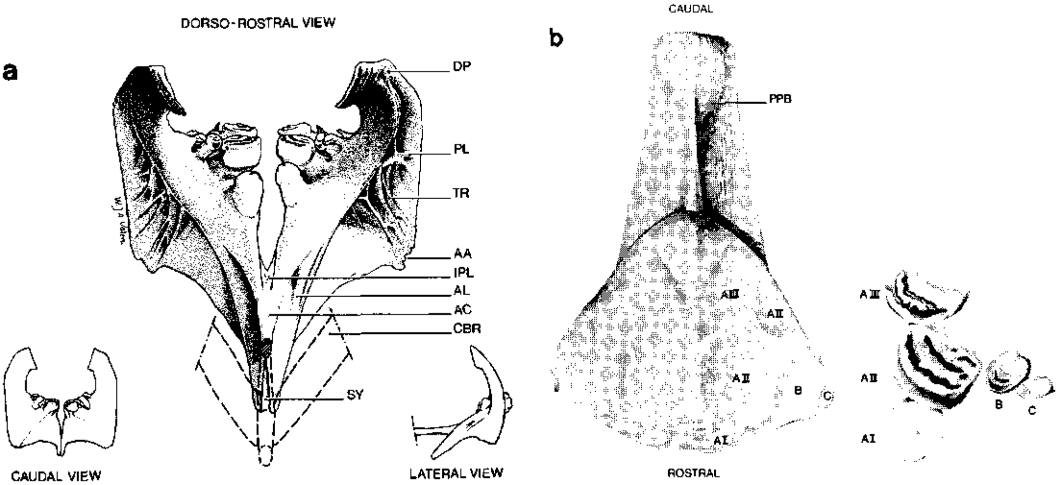


Fig. 2. a. Pharyngeal bones and teeth. b. Ventral view of the chewing pad and the pharyngeal process. A dorsal view of pharyngeal teeth for comparison at the same scale. Note the pitted anterior surface of the chewing pad, reflecting the crushing action of the A I teeth, and the grinding facets of the corresponding furrowed teeth.

which are absorbed in the base of the skull. The dorsal arches give rise to the Weberian ossicles.

The occlusal surface of the chewing pad is divided into slightly concave halves by a medial ridge that projects most ventrad posteriorly. Both areas show distinct traces of abrasion by the corresponding A II, A III, B, and C teeth. Owing to the low position of A I, occlusal contact of this tooth with the chewing pad is commonly denied in the literature (e.g., Geyer, '37); a rough rostral region on the chewing pad is, however, conspicuous.

2. Ligaments, articulations, and movement restrictions

Ligaments. A meshwork of interpharyngeal ligaments connects the pharyngeal bones along their anterior limb in the midline (Fig. 6). The ligaments extend from the symphysis and the rostromedial part of the one bone to the caudomedial part of the other, intercrossing from both sides at 30-40°. Caudal ligaments are continuous with the rostral aponeurosis and the medial raphe of the transversus ventralis V muscles, which interconnect the bones at their anterior angles.

The ligament of Baudelot, a stout and flat upright ligament, runs in transverse and slightly caudal direction from the ventromedial part of the skull (at the rostral margin of the basioccipital process) to the medial surface of cleithrum and supracleithrum (Figs. 3, 5). It lies posterior to the dorsal process of the pharyngeal bone and is continuous with the most anterior myosept of the epaxial muscles.

The membrane covering the free lateral surface of the pharyngeal bones thickens toward the cleithrum, especially along the posterior limb. It will be called the pharyngocleithral membrane.

Articulations. The only "articulation" of the pharyngeal bones is their fibrous connection to the anterior cartilage (Figs. 1, 5). The oval posterior head of this copula fits into a shallow pit, formed by the joined dorsomedial surfaces of the pharyngeal bones and the interconnecting tissues (Fig. 2a); the smooth anterior head of the cartilage slides rostrocaudad over the posterior slope of basibranchial III; the rostral part of the latter limits these movements (Fig. 5).

Movement axes and limitations. Extrinsic movements of the pharyngeal bones (joint movements with respect to surrounding elements) are limited most directly by the attached branchial basket, the pharyngocleithral membrane, and the collagen components in the pharyngeal muscles. If a fixed position is assumed for the branchial basket, translation of the bones can only be small; it depends largely on the sliding of the anterior cartilage over basibranchial III, and on the slack in the branchial interconnections and the pharyngocleithral membrane. As soon as this slack is absorbed, increasing forces on the pharyngeal bones lead to rotation around a transversal axis R^1 (Fig. 3). This rotation is limited by tissue connecting the pharyngeal bones and the branchial basket. Caudad translation of the pharyngeal bones is ultimately obstructed by Baudelot's ligaments (Fig. 3); continued retraction produces an almost sagittal rotation with the point of abutment as the new center. The ligament as a whole becomes the transversal R^4 axis. (During mastication of large food particles the instantaneous center of rotation may well lie between teeth and chewing pad.) Large excursions of the pharyngeal bones around R^4 can only proceed with concomitant movement of both the branchial basket and the pectoral girdle.

Movements of the pharyngeal bones with respect to each other are the intrinsic movements. Intrinsic translations are virtually impeded by the symphysis. Rotations are permitted around a rather longitudinal hinge-like axis through symphysis and interpharyngeal ligaments (R^2 in Fig. 3). (A reconstruction of pharyngeal bone movements in lateral projection shows the anterior angle (B in Fig. 8a) to move at right angles to this R^2 axis and confirms its assumed position.) In order to analyze and describe other intrinsic movements, the definition of further axes is useful. Other rotations of the two bones are small and only possible as far as permitted by the interpharyngeal ligaments; when they occur in the plane of these ligaments, the excursion is maximal, and an axis R^3 can be postulated at right angles to R^2 and R^1.

3. Myology (Figs. 4-7)

Eastman ('71) reviewed the nomenclature of the pharyngeal bone muscles of previous authors. Following his description in detail, the m. coraco-branchialis posterior and the m. cleithro-pharyngeus profundus evidently correspond, respectively, to the m. coraco-branchialis anterior and posterior as described by Matthes ('63) and others (see Table 1). This error crept into the literature review and renders it highly confusing at this point. In this paper the nomenclature as used by East-

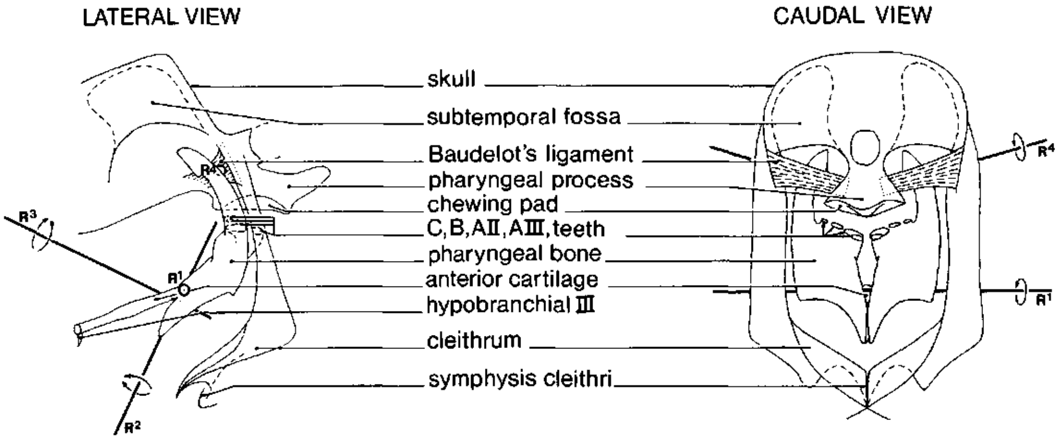


Fig. 3. Rotation axes in the masticatory construction. The range of pharyngeal bone movements and their limitations are described in the text. This scheme serves Figure 7 also.

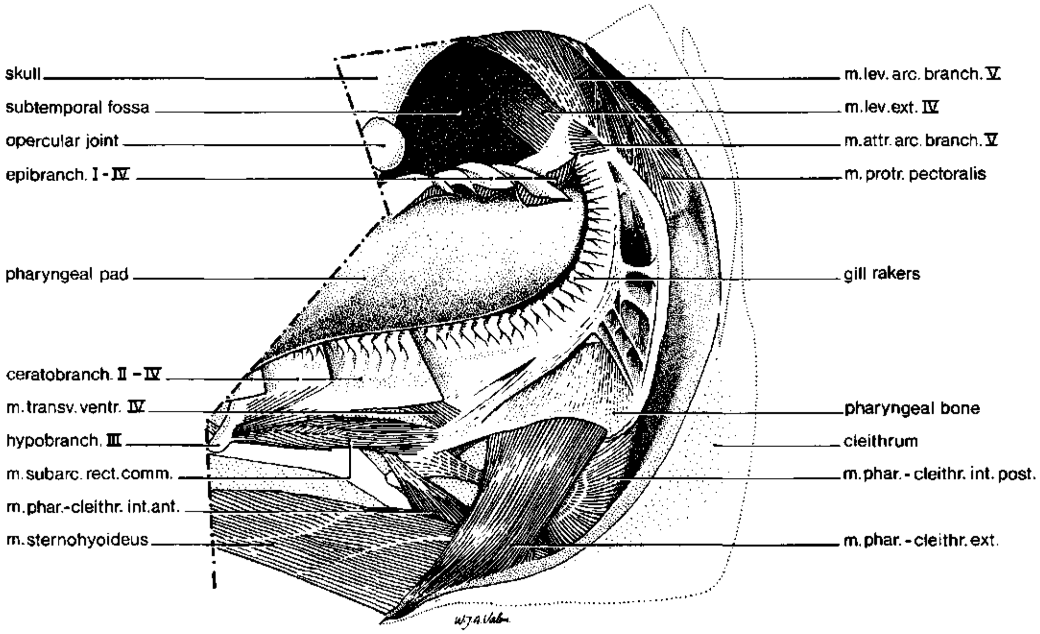


Fig. 4. Lateral view into the anterior pharynx showing the left pharyngeal bone and its musculature; the opercula and most of the branchial arches have been removed. At rest, the thick dorsal pharyngeal pad almost fills the pharyngeal lumen; it is muscular and covered with mucous cells and taste buds. Full names of the muscles in the descriptive part of the text.

TABLE 1. Nomenclature of the pharyngeal bone muscles of cyprinids as applied by selected authors

Name used in this paper	Eastman ('71)	Matthes ('63)	Takahasi ('25)	Winterbottom ('74)
levator arcus branchialis V (LAB V)	levator arcus branchialis V	levator arcus branchialis V	trapezius profundus	levator posterior
retractor os pharyngeus	retractor os pharyngeus	retractor arcus branchialis dorsalis	retractor arcus branchialis dorsalis	retractor pharyngeus
superior (ROPS)	superior	superior	superior	superior
inferior (ROPI)	inferior	inferior	inferior	inferior
pharyngo-cleithralis externus (PCE)	cleithro-pharyngeus superficialis[1]	cleithro-pharyngeus (superf. + profund.)	pharyngo-clavicularis externus (superf. + profund.)	pharyngo-clavicularis externus
pharyngo-cleithralis internus posterior (PCIP)	cleithro-pharyngeus profundus[1]	coraco-branchialis posterior	pharyngo-clavicularis internus posterior	pharyngo-clavicularis internus posterior
pharyngo-cleithralis internus anterior (PCIA)	coraco-branchialis posterior[1]	coraco-branchialis anterior	pharyngo-clavicularis internus anterior	pharyngo-clavicularis internus anterior
transversus ventralis V (TV V)	transversus ventralis V	transversus ventralis V	transversus ventralis V	transversus ventralis
subarcualis rectus communis (SRC)	subarcualis rectus communis	subarcualis rectus communis	pharyngo-arcualis hyoideus	rectus communis
attractor arcus branchialis V (AAB V)	–	attractor arcus branchialis posterior	adductor arcus branchialis posterior	adductor V
obliquus posterior (OP)	–	–	obliquus dorsalis superioris (part III)	obliquus posterior
constrictor pharyngis (CP) (anterior part sphincter oesophagi)	–	constrictor pharyngis (anterior part sphincter oesophagi)	constrictor pharyngis	sphincter oesophagi

[1] These muscles were erroneously named; see text.

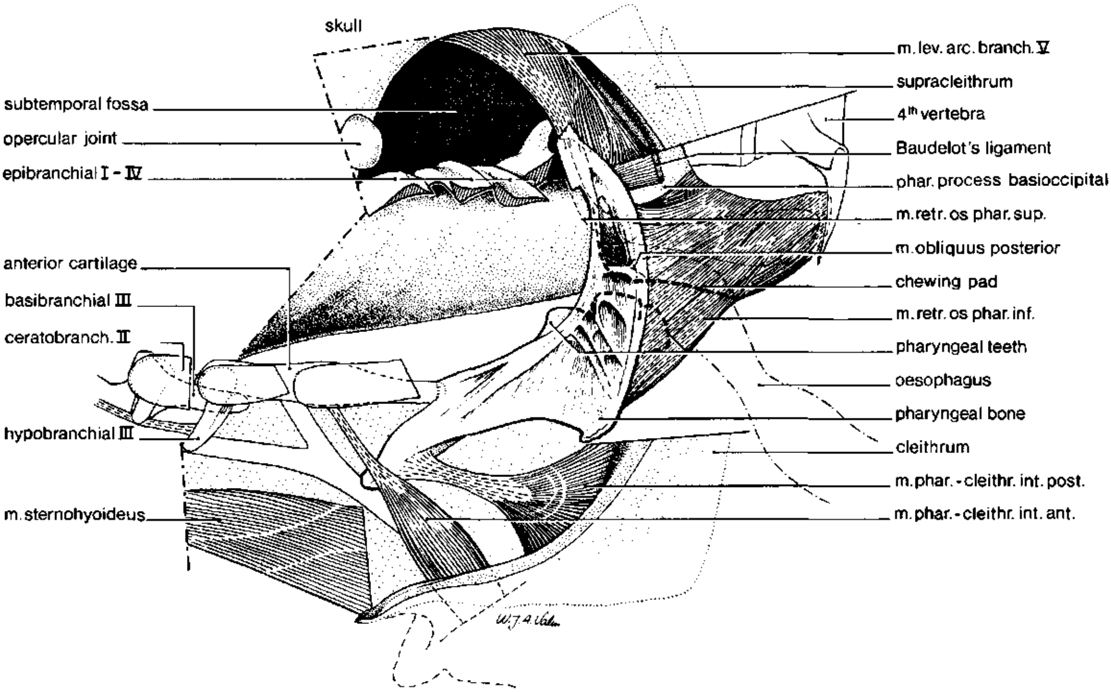
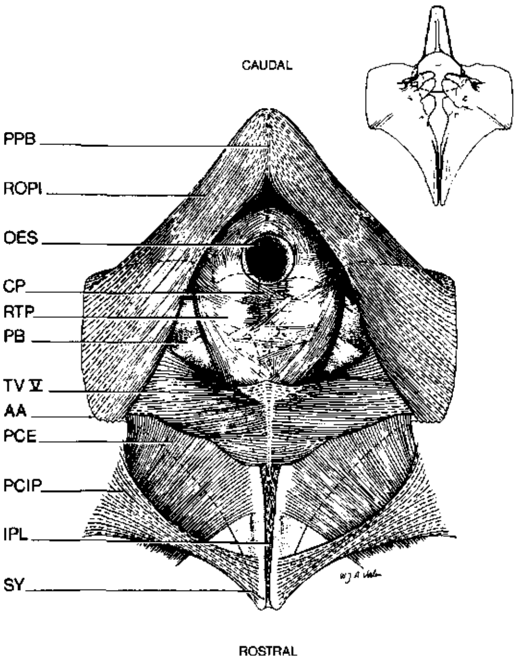


Fig. 5. Deep dissection of the anterior pharynx. Partial removal of the lateral body wall permits a view on the wall of the posterior pharynx, between teeth and chewing pad. Note the stout ligament of Baudelot, the slide-coupling between the anterior cartilage and basibranchial III, and the tendinous character of the LAB V and PCIP muscles.

man ('71) is further followed. The coracobranchial muscles, however, are incorporated in the m. pharyngo-clavicularis (Winterbottom, '74; this author gives an excellent synonymy of teleost muscles), modified to m. pharyngo-cleithralis (following Liem, '70) because a clavicle is absent in teleosts.

Brief descriptions of all pharyngeal bone muscles are given below. For details the reader is referred to the figures. The contraction ef-



Abbreviations

CP, m. constrictor pharyngis
OES, oesophagus
PB, pharyngeal bone
PCE, m. pharyngo-cleithralis externus
PCIP, m. pharyngo-cleithralis internus posterior
ROPI, m. retractor os pharyngeus inferior
RTP, replace-tooth patch
TV V, m. transversus ventralis V

Fig. 6. Ventrocaudal view of the pharyngeal bones and related structures. Broken lines indicate the pharyngeal bones as figured with the chewing pad at the upper right. Note the cruciate pattern of the interpharyngeal ligaments. The constrictor pharyngis muscle is part of the wall and floor of the posterior pharynx.

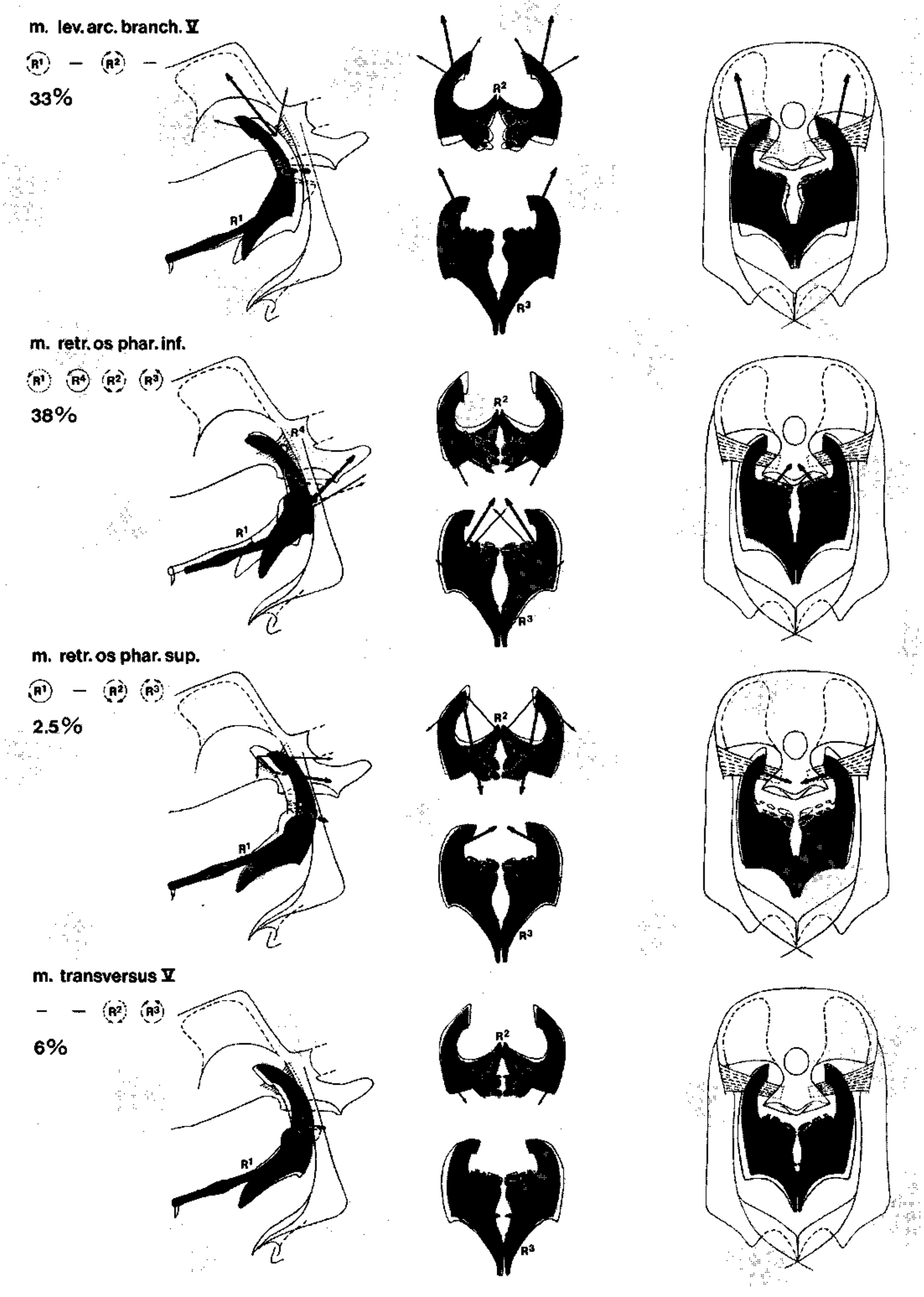
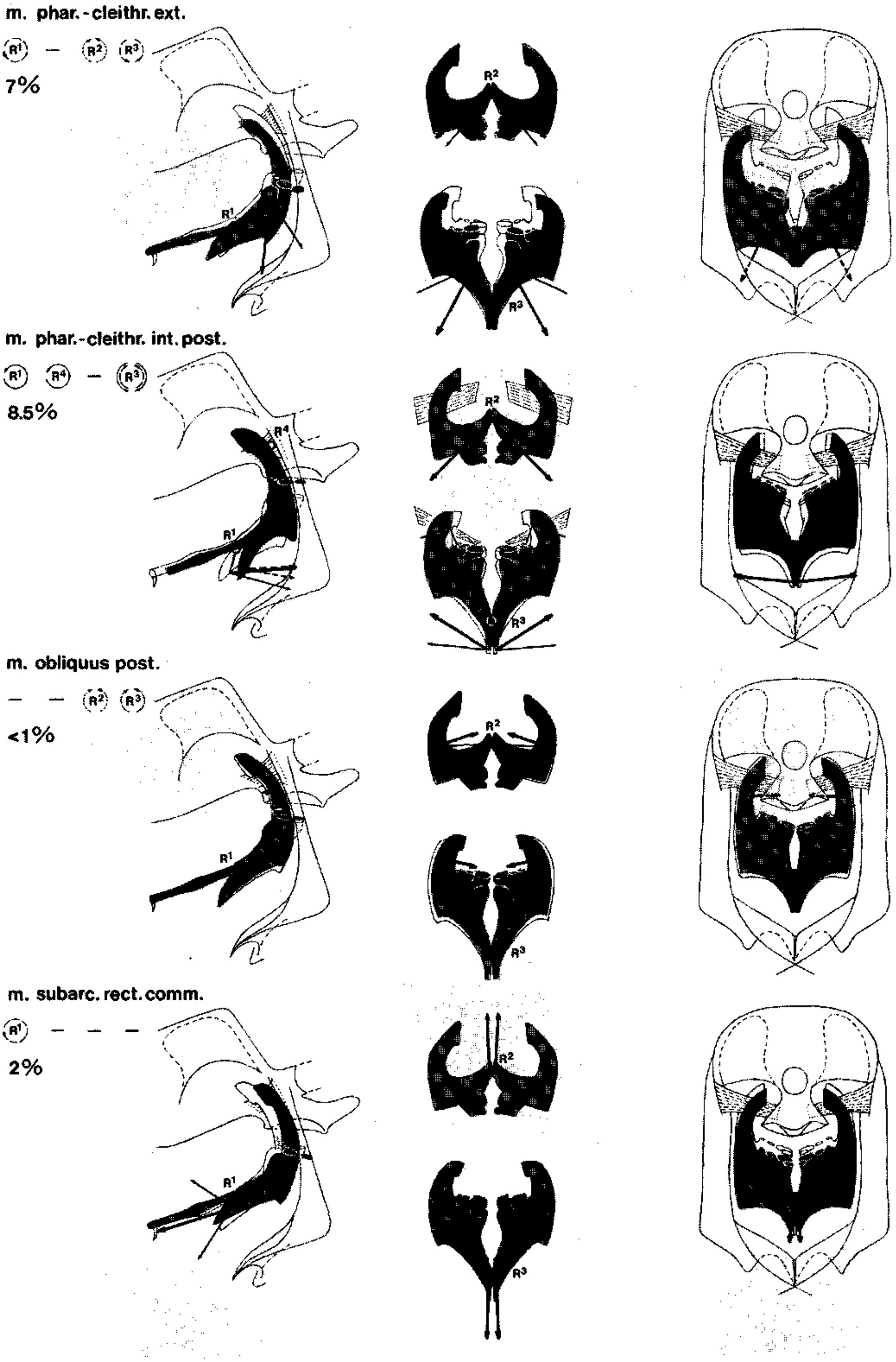


Fig. 7. a (left) and b (right). Separate contraction effects of the single pairs of muscles on the position of the pharyngeal bones and teeth (grey image), based on anatomical data. White image indicates rest position. Skull, branchial basket, and pectoral girdle are maintained motionless. Effects depicted in three planes, at right angles to the separate axes. A caudal view on the construction aids visualization. Percentages indicate the share of each muscle pair in the total weight of pharyngeal bone muscles. Forces correspond to the lines of action, and are resolved in rotation components



around the individual axes, and in remaining translation components. Rotation effects have been noted in code: Arrows around "R" indicate direction and intensity of rotation. The direction of simultaneous translation components are to be traced from the schemes. Translational forces may load the symphysis of the pharyngeal bones by compression or tension (cf. TV V, PCE). For further details, see text. Structures and axes indicated in Figure 3.

fects of the separate pairs of muscle on the position of the pharyngeal bones and teeth, based on anatomical data as action-lines and movement restrictions, are shown in Figure 7. These effects will differ from the actual effects in the living fish because simultaneous actions of other muscles have not been taken into consideration; the position of the branchial basket and pectoral girdle, for example, is kept fixed. For most muscles the wet weight as a percentage of the total weight of the pharyngeal bone musculature is indicated; differences in their share are large.

M. levator arcus branchialis V (LAB V; Figs. 4, 5, 7). The fan-shaped LAB V is large (33%), originates from the deep subtemporal fossa of the skull, and inserts on the posterior surface of the dorsal process of the pharyngeal bone. Its anterior part is highly aponeurotic.

Action. The LAB V muscles rotate the pharyngeal bones powerfully anticlockwise around the R^1 axis; at the same time they move them right to the chewing pad. They also abduct the bones around R^2. The pharyngeal teeth move dorsad and slightly rostrad toward the chewing pad; they are abducted.

M. retractor os pharyngeus inferior (ROPI; Figs. 5–7). The ROPI originates tendinously from the posterior part of the basioccipital pharyngeal process. It is inserted on the posterior limb of the pharyngeal bones, ventral to the LAB V insertion. This large muscle (38%) contains many aponeurotic elements. Neither this muscle nor the ROPS (see below) is homologous with branchial muscles, because they arise from the sphincter oesophagi (Holstvoogd, '65; Nelson, '67).

Action. The pharyngeal bones are retracted and rotate slightly anticlockwise around the R^1 axis. Because retraction is blocked by Baudelot's ligaments, powerful rotation is induced around this ligament (R^4) (broken vectors in Fig. 7). Translation toward the chewing pad is small. The powerful ROPI is the main adductor (around R^3 and R^2) of the bones. Pharyngeal teeth are adducted and move dorsocaudad against the chewing pad.

M. retractor os pharyngeus superior (ROPS; Figs. 5, 7). The long but thin ROPS (2.5%) originates just anterior of the ROPI on the pharyngeal process. Fibers converge on tendinous strands that run rostrad, medial of the dorsal process of the pharyngeal bone, and are inserted with a dorsad curving tendon on its dorsal tip.

Action. The pharyngeal bones rotate mainly clockwise around the R^1 axis; this is accompanied by adduction around R^2 and R^3. Pharyngeal teeth are adducted. They move caudad and slightly away from the chewing pad.

M. transversus ventralis V (TV V; Figs. 6, 7). The paired TV V (6%) spans the pharyngeal bones ventrally at their anterior angles, just anterior to the teeth. Fibers of both sides meet in a medial "raphe," which has a connection with the interpharyngeal ligaments. These are, together with the constrictor pharyngis, the only intrinsic muscles of the pharyngeal bones and they form a part of the pericardial roof. Muscle fibers originating from the medial aspect of the anterior limb as described by Eastman ('71) have not been found.

Action. Some components adduct the pharyngeal bones around the R^2 and the R^3 axis. Other components press them together at the symphysis. Pharyngeal teeth are adducted.

M. pharyngo-cleithralis externus (PCE; Figs. 4, 6, 7). The thin, parallel-fibered PCE (7%) interconnects the horizontal limb of the cleithrum and the ventromedial edge of the pharyngeal bone, anterior to the teeth. Some deeper fibers are inserted more anteriorly on the bone and cross below the superficial fibers at an angle of about 30°. In the carp the distinction between a separate superficialis and profundus part is less conspicuous.

Action. The PCE muscles protract and simultaneously rotate the pharyngeal bones clockwise (R^1). Abduction of the pharyngeal bones proceeds around the R^3 axis mainly. Pharyngeal teeth abduct and move away from the chewing pad.

M. pharyngo-cleithralis internus anterior (PCIA; Figs. 4, 5). The small, conical PCIA (1.5%) originates from the medial part of the pectoral girdle, passes along the symphysis of the pharyngeal bones, and is inserted through a tendon to the ventral surface of the anterior cartilage between the ceratobranchials IV.

Action. By lowering the anterior cartilage, the PCIA muscles only indirectly move the pharyngeal bones (therefore not shown in Fig. 7); the PCIA might even depress the symphysis, held between the PCIA tendons. Contraction causes a minor anticlockwise rotation in a sagittal plane. Pharyngeal teeth move slightly toward the chewing pad.

M. pharyngo-cleithralis internus posterior (PCIP; Figs. 4–7). The PCIP (8.5%) lies medial to the sternohyoid muscle, posterior to the PCIA. It has an extensive origin on the dorsal cleithral surface at the bending of the horizontal into the vertical limb. Muscle fibers sharply converge through aponeuroses on a heavy tendon that continues rostromediad and is inserted on the symphysis of the pharyngeal bones. Some medial fibers originate medial to the cleithrum from the hypaxial body muscles (intercostal fibers; cf. Brousseau, '76) with which they are continuous; only aponeurotic elements are interposed.

Action. The anticlockwise rotation of the pharyngeal bones around the R^1 axis is soon limited by their attachment to the branchial basket; the PCIP muscles, then, are pure retractors. Just as described for the ROPI muscles, the presence of Baudelot's ligaments transforms the retraction of the bones into a rotation around R^4 (broken vectors in Fig. 7). Because the lateral attachments of these ligaments lie posteriorly to the medial ones, the dorsal processes of the bones are forced to slide laterad. This causes abduction around R^3. Pharyngeal teeth move dorsocaudad against the chewing pad and will be abducted.

M. obliquus posterior (OP; Figs. 5, 7). The OP (less than 1%) originates medially on the basioccipital process just dorsal to the anterior margin of the chewing pad. It runs laterad along the medial surface of the posterior limb of the pharyngeal bones and is attached on its posterior surface between the LAB V and ROPI insertions. Both origin and insertion of this small muscle are fleshy.

Action. The OP muscles adduct the pharyngeal bones around R^3 and cause compression in the symphysis. Teeth are adducted also.

M. subarcualis rectus communis (SRC; Figs. 4, 7). This long, cylindrical muscle (2%) lies midventral in the branchial basket, parallel to the anterior cartilage. It connects the anterolateral surface of the pharyngeal bone to the posterior surface of hypobranchial III. Some internal aponeuroses occur. Few fibers may well be attached to the ventral surface of ceratobranchial IV; fibers to basibranchial III, as reported by Eastman ('71), have not been found.

Action. Apart from clockwise rotation of the pharyngeal bones around the R^1 axis, the SRC muscles protract and slightly depress them. The pharyngeal teeth move away from the chewing pad.

M. constrictor pharyngis (CP; Fig. 6). As the anterior part of the sphincter oesophagi, the CP contributes to the wall and floor of the posterior pharynx between teeth and chewing pad. The CP lies medial to the ROPI and consists of multiple fiber groups running in various directions. Anteriorly, they are inserted on the medial aspects of the pharyngeal bones and on the basioccipital process along the chewing pad. Posteriorly the CP is continuous with the esophagus. (Patches of lightly colored tissue between the fibers indicate new teeth, developing in the floor of the posterior pharynx.)

Action. They constrict the posterior pharynx. In addition, the CP action resembles that of the ROPI muscles.

M. attractor arcus branchialis V (AAB V) and M. transversus ventralis IV (TV IV) (Fig. 4). The AAB V and TV IV (both less than 1%) are short, parallel-fibered muscles with their origin on the pharyngeal bones. The AAB V runs rostrad from the dorsal tip of the pharyngeal bone to the epibranchial IV. The TV IV passes rostrodorsad from the anterolateral surface of its horizontal limb, dorsal of the SRC, to the ceratobranchial IV. They play a minor role in positioning them and therefore have been omitted in Figure 7.

Head muscles other than the pharyngeal bone musculature are mentioned in the text. These are described by Ballintijn ('69a), who determined their role in the respiration of the carp. The lines of action of the most relevant muscles are indicated by bold lines in Figure 1.

Feeding ecology of the carp

The carp typically ingests the food by suction (pipette-feeding; Gosline, '73) with the highly protrusible, subterminal, and toothless mouth. The fish can penetrate more than 12 cm into a silty bottom (Suietov, '39). Apart from food, inert and anorganic material enters the mouth as a part of the ingested medium, and only a part of this is prevented from entering the digestive tract, as indicated by the sandy intestinal contents. Thus, pharyngeal selection is restricted. Expulsion of waste material takes place through the branchial sieve or through the mouth by a spitting movement, causing a fast and reversed water current. The thick dorsal pharyngeal roof (Fig. 4) (called by some the pharyngeal pad, and by others the palatal organ), provided with numerous taste buds and mucous cells, may play an active role in selecting food by a lesser affinity of inorganic compounds to its mucus as a result of surface-tension phenomena (Matthes, '63) and by its contractility. The branchial filter can retain particles larger than 500 μm and plays a major role in straining algae (Uribe-Zamora, '75). After mastication the food is swallowed and digested in an alimentary tract lacking a stomach; the esophagus passes through a sphincter directly into the intestine, as in all other cyprinids.

Food of the carp

The carp's diet has been investigated repeatedly, mainly in fish ponds, in many parts of the world. Uribe-Zamora ('75) reviewed these data for larval and adult fish.

The diet of the adult carp varies according to the season:

Winter: Feeding activity is reduced and restricted to the benthos that is most abundant at that time and includes chironomid larvae and tubificids. At temperatures below 8 °C, feeding is minimal or ceases completely.

Spring: The zooplankton proliferates; the carp leaves the bottom areas and feeds on the larger crustaceans (*Diaptomus castor, Daphnia longispina,* and *Cyclops bohater*).

Summer: Large-sized zooplankton are less abundant and the carp feeds on littoral vegetation, especially soft species such as *Lemna minor* and *Glyceria fluitans*, and on the fauna between these macrophytes: molluscs, copepods, trichopter larvae, and phytophyl oligochaets such as *Lumbricus variegatus*.

Autumn: When the oxygenation of open water increases again, the carp returns to the benthic areas to feed on dipters such as *Chaoborus flavicans*, that reaches maximal abundance at the end of the summer, and on oligochaets. The diet may include small planktonic crustaceans, larger zooplankton is scarce.

Thus, carps are omnivorous, euryphagous and opportunistic fishes, feeding in diversified ecological areas and at different depths. A differentiation of the diet into basic, secondary and incidental food (Nikolsky, '63) is hardly justified.

Effect of mastication on food items

Examination of the intestinal contents and feces by Klust ('40) and by the present author reveals that *earthworms* usually are squashed and punctured, thereby exposing the internal organs of the worm to the digestive juices of the carp. This suggests action of the pointed A I teeth. *Tubificids* are partly squashed if offered individually; when ingested as a mass they are hardly damaged (Klust, '40). According to Klust ('40) *chironomid* larvae are not damaged, owing to their tough chitinous skeletons. Examination of feces shows, however, holes between the segments of the flattened and crumpled larvae; this permits digestive fluids to enter the larva. Usually the separate skeletons are identified easily. The carapace of *Daphnia* and other planktonic crustaceans appeared to be crushed (Klust, '40). Fecal pellets of carps fed on bivalved *molluscs* (sphaeriids) mainly contain shell fragments. Ordinary *grass*, ingested by young carps in our laboratory, shows disruptions of the fibrous context; the grass appears to be repeatedly squashed and cells are washed out. Considerable areas remain unaffected. *Barley* fed to carps of yearclass-II and stored hard maize fed to yearclass-III carps are pulverized. Intestinal examination reveals large and minute fragments. The feces contain mainly indigestible seed capsule elements.

Experimental results

1. Measuring procedure

Movement analysis. Movement analysis included the measuring of distances and angles in sagittal and horizontal X-ray projection, as illustrated in Figure 8. Positional changes of the markers in successive X-ray frames are the resultant effect of both translations and rotations around the R^1, R^2, R^3, and R^4 axes. In order to determine these components in the small movements recorded, the location of the measuring marks and the procedure of measuring were designed to produce high excursions for the component to be measured, a low sensitivity for other movements, and a maximal expression in the plane of projection. For the measuring marks A, B, and C on the pharyngeal bone (Fig. 8) each of the possible movement components has been simulated and the effects in projection evaluated for obtaining selective measurements.

Skull movements around a center shifting between the first and the fourth vertebra (R^v in Fig. 8a) play a major role in mastication. Therefore, a distinction is made between *relative* movements of teeth and other head structures, those with respect to the skull, and *absolute* movements, related to the axis of the body. This axis is always approximated by the position of the swimm-bladder and the vertebrae lying above, because these structures contrast well in X-ray images and their projections are not distorted by roll of the fish. To obtain the absolute pharyngeal bone rotation, rotation of the skull ($\Delta\sigma$ in Fig. 8a) is subtracted from $\Delta\alpha$; the same applies to the absolute rotation of the pectoral girdle; however, owing to the caudad movement of R^p when the skull is lifted (Fig. 8a), only $\frac{1}{2}\Delta\sigma$ is to be subtracted from $\Delta\beta$ (determined empirically).

Electromyograms. To obtain a typical and complete pattern of masticatory activity, the electromyograms of different muscles in various experiments were combined; this was done by recording permanently three masticatory muscles (LAB V, PCE, and SRC), active in dif-

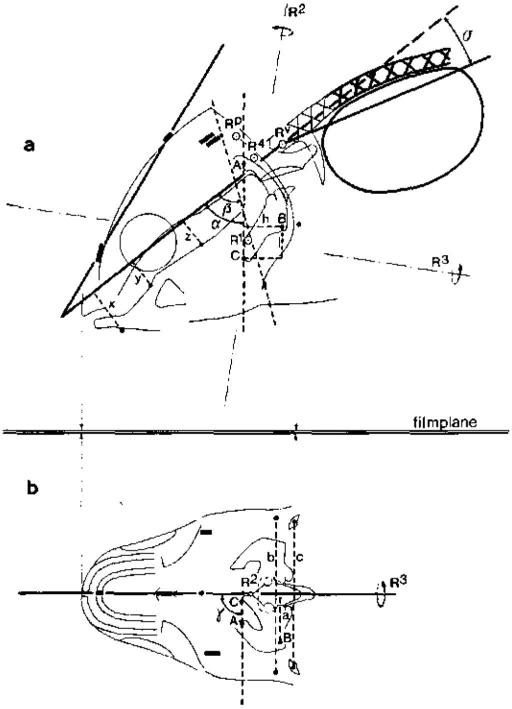


Fig. 8. Corresponding sagittal (a) and horizontal (b) projection schemes as framework for selectively measuring movements. Reference elements are heavy; measuring lines dotted. (–, reference mark; •, measuring mark). Rotation axes indicated.

a. Symbols: σ, skull movement relative to the body (R^V); α, angle between pharyngeal bone and skull (R^1 and R^4); β, angle between pectoral girdle and skull (R^P); x, distance lower jaw to the skull; y, compression buccal cavity; z, compression anterior pharynx; h, adduction phar. bones (R^2); l, adduction phar. bones (R^3).

b. Symbols: γ, rotation phar. bone in the sagittal plane; a, adduction phar. bones (R^2 + R^3); b, adduction opercula; c, adduction pectoral girdle.

ferent phases of the masticatory cycle (see below). Variation in the duration of the masticatory cycle is caused to a large extent by variation in the PCE activity between successive power strokes (Fig. 9). Activity periods of different cycles, therefore, have been compared with respect to the LAB V activity period in the corresponding power stroke. Durations of the activity periods in Figure 14 represent mean values. During X-ray cinematography, the activity of the LAB V, PCE, SRC, and LOP (levator operculi) muscles was recorded in order to correlate movements to the overall EMG pattern.

2. Terminology

A masticatory *sequence* comprises all activities involved in the mastication of a food bolus (Fig. 9), and is composed of one or more *trains* of rhythmic masticatory *cycles*, separated by masticatory *pauses*. Within a continuous train (e.g., cycle I–X in Fig. 10) the profile of the individual cycles may change, resulting in different masticatory *series* (cycles I–V and VI–X in Fig. 10).

For the masticatory cycle of the carp the following definitions will be used:

a. During the *preparatory* stroke the intermediate gape between the occlusal surfaces increases to a maximum to allow the food to be masticated, and the occlusal surfaces are brought in a favorable position for comminution.

b. In the *power* stroke the occlusal surfaces approach each other, resulting in tooth–food–chewing pad contact and the oft-sustained application of high forces on the food. Given their morphology (Fig. 2) *crushing* is effected when the occlusal surfaces approach each other perpendicular to these surfaces, *grinding* when the occluded surfaces move parallel to each other.

c. The *recovery* stroke starts when tooth–food–chewing pad contact is broken. The distance between the occlusal surfaces increases and the pharyngeal bones and teeth move to an intermediate rest position, thus not obstructing other movements of the branchial basket.

Contrary to the usage in papers on mammalian mastication (Hiiemae, '78), fast closing of the occlusal surfaces is included in the power stroke.

3. Masticatory movements

The power stroke of the masticatory cycle (cycle VII in Fig. 10) is an anticlockwise rotation of the pharyngeal bones with respect to the skull (increase of α; see Fig. 8a), which moves the teeth vertically as well as in a direction parallel to the chewing pad. Between two power strokes, we find the recovery and the preparatory stroke of the two successive cycles; the transition is marked by changes in the rotation velocity (α) and, later in the sequence, by the arise of a pause in the PCE activity (Fig. 10; cycle VIII–IX). This interpretation is supported by the EMGs of more isolated cycles, in which a complete pause is noticed in the PCE activity (□, ● in Fig. 9).

Two related profiles of masticatory cycles are distinguished by movement and EMG pattern: a crushing cycle (Fig. 10; I–IV) and a grinding cycle (VI–X). The latter will be discussed first, in relation to Figures 11 and 12, which summarize movement data from sagit-

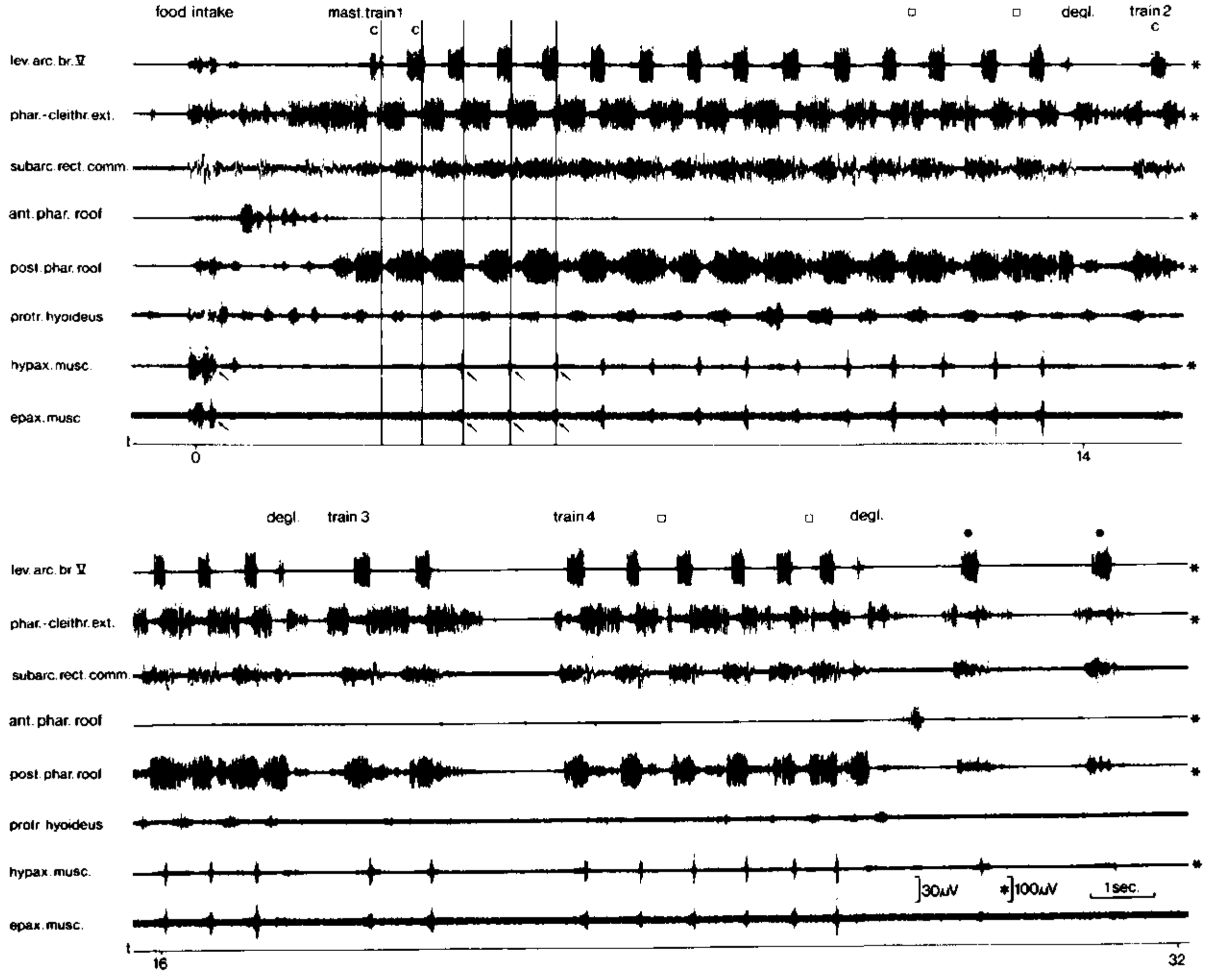


Fig. 9. Joined action of pharyngeal bone, head, and body muscles during food transport and mastication in the carp. The masticatory sequence is composed of four trains and some individual cycles (●). First train includes a series of crushing (c) and a series of grinding cycles, and is completed by deglutition (cf. Fig. 17). The power stroke corresponds to the period of LAB V activity. Note that the variation in cycle time is mainly caused by the PCE. In the course of the sequence, the period of high PCE activity breaks up (□) into parts of the successive cycles. Note also the transition of activity from the anterior to the posterior pharyngeal roof after food pellets intake, indicating its role in food transport. The body muscles participate in food intake and grinding (arrows), whereas at crushing their activity is low

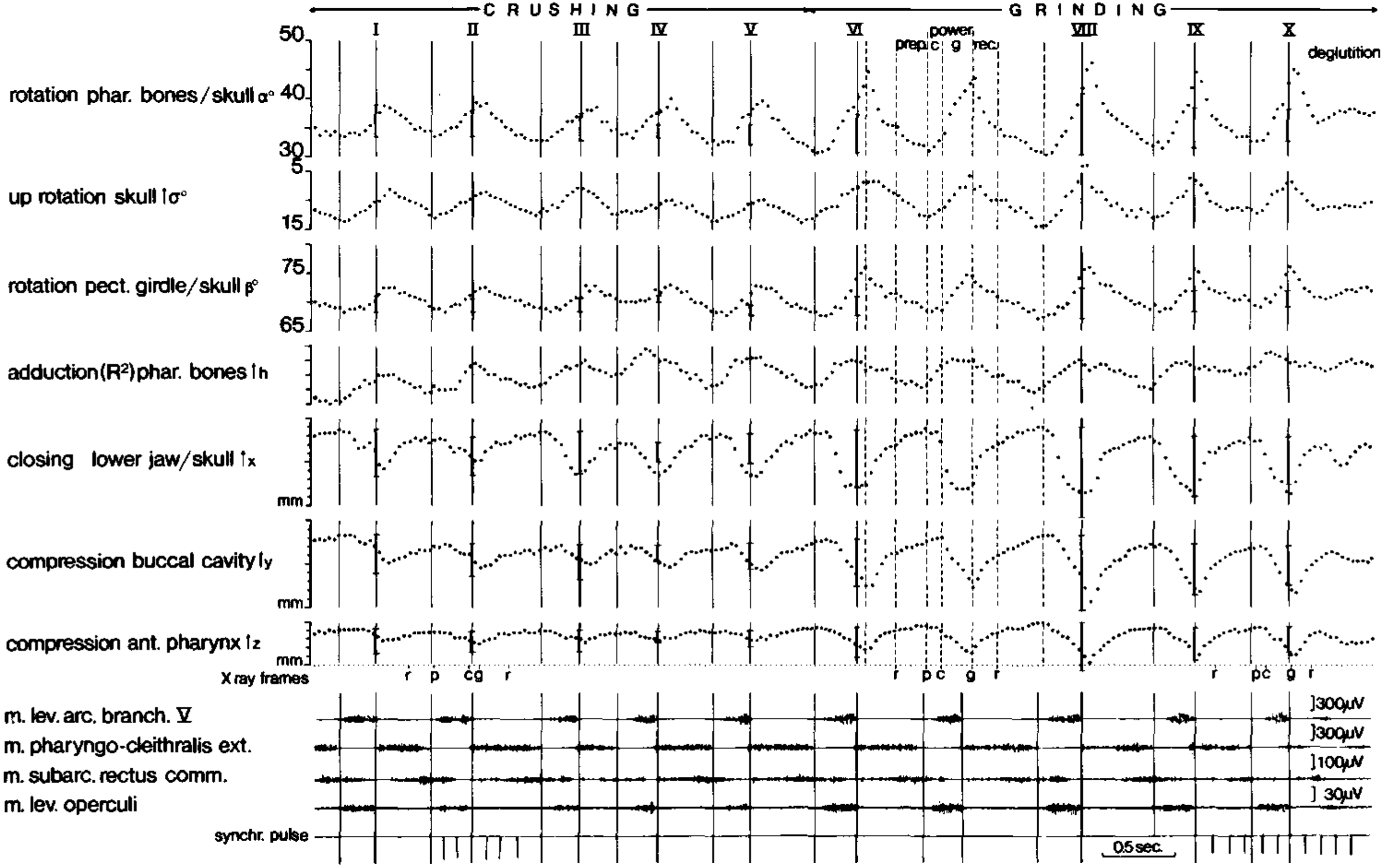


Fig. 10. Cyclic movements of head elements during the first train of a masticatory sequence in a feeding carp (pellets), measured in lateral X-ray films. Simultaneous EMGs of pharyngeal bone muscles permit comparison with the overall EMG pattern (Fig. 14). Vertical lines mark termination of LAB V or PCE activity. First series (I–V; small amplitudes) represent crushing cycles, second series (VI–X; large amplitudes) grinding cycles. Cycle VII is subdivided into a preparatory (prep), crushing (c), grinding (g), and recovery (rec) stroke. In grinding the crushing phase is shortened and the grinding phase extended, compared to crushing (cf. cycle II). Pharyngeal bone abduction in the power stroke is more pronounced at grinding. Note the large share of skull rotation (σ) in most movements, indicated by heavy bars on the vertical lines. Expansion of the buccopharyngeal cavity is extensive and synchronous with the power stroke. Symbols according to Figure 8a.

tal and horizontal projections. Some original recordings will be referenced.

Grinding cycle. Starting from an intermediate rest position during the *preparatory stroke* (p), the pharyngeal bones are slightly protracted and they rotate clockwise with respect to the skull (Figs. 11a, 12), thus expanding the posterior pharynx between teeth and chewing pad to admit or adjust the food to the occlusal surfaces. At the same time the anterior pharynx is compressed (Figs. 11c, 12) and this causes a caudad pumping action. Apart from the rotation of the pharyngeal bones, facilitated by a slight protraction of the pectoral girdle (Figs. 11b, 12), a down-rotation of the skull contributes to these effects. Meanwhile the pharyngeal bones are fully abducted and they finally initiate an adduction, turning the mediad-pointing teeth dorsad for crushing. The preparatory effect of these movements is demonstrated distinctly in a masticatory sequence (Fig. 13) in which the fish, with the pharyngeal bones kept abducted, fails to bring a large food pellet on the teeth (revealed by the X-ray movie). At a second attempt the preparatory stroke is intensified: The anterior pharynx is fully compressed and the posterior pharynx expanded (very small α).

The transition from the preparatory stroke (p) into the *power stroke* is initiated by the adduction, lifting, and moderate anticlockwise rotation (R^1) of the pharyngeal bones, thus bringing the teeth closer to each other and to the chewing pad (Figs. 11, 12). Up-rotation of the skull contributes significantly to occlusion by the dorsad movement of the skull-suspended pharyngeal bones and their teeth. Because the chewing pad lies close and ventral to the rotation center of the skull (R^v in Fig. 8), it is not lifted but rotates slightly rostrad. As the movement of the teeth is perpendicular to the chewing pad, this part of the power stroke is the *crushing phase* (c). Although the skull is lifted, the anterior pharynx remains fully compressed (cf. Fig. 13, cycle I); this implies the lifting of the pharyngeal floor during the crushing phase, thus fixing the food to be crushed. Also the pectoral girdle is slightly lifted with the skull (Fig. 12).

As the power stroke proceeds, skull-rotation and thus lifting forces on the teeth perpendicular to the chewing pad continue (Figs. 11a, 12). The pharyngeal bones move at the same time caudad, but their dorsal tips are blocked soon by Baudelot's ligaments (cf. Sibbing, '76; masticatory orbit of the pharyngeal bone); this forces the bones into an increasing anticlockwise rotation (α), but now around R^4. The pharyngeal teeth describe a circle segment around R^4 and move more parallel to the chewing pad. This represents the *grinding phase* (g) of the power stroke. Because the chewing pad declines ventrad posteriorly, the food is increasingly compressed and wedged more and more between teeth and chewing pad during the grinding phase. The pharyngeal bones may remain adducted now, but often abduct to a varied extent. The extensive rotation of the pharyngeal bones around Baudelot's ligaments is permitted and supported by a distinct retraction of the pectoral girdle and a depression of the pharyngeal floor (Figs. 11, 12). With progressive lifting of the skull, this produces an explosive expansion of the anterior pharynx during the grinding stroke. The angular velocity of the pharyngeal bones with respect to the skull is about 60°/sec during the power stroke and resembles the value of 64°/sec found by Hiiemae ('76) for the opossum lower jaw.

The *recovery stroke* (r) starts with the loss of occlusal contact and the lowering of the pharyngeal teeth by clockwise rotation and depression of the pharyngeal bones (Figs. 11, 12), accompanied by down-rotation of the skull, and leads to compression of the anterior and expansion of the posterior pharynx, to an extent comparable to quiet respiration. Abduction of the pharyngeal bones continues in the recovery stroke and the pectoral girdle returns forward.

Crushing cycle. The typical crushing cycle differs from the grinding cycle mainly by the predominance of the vertical movements of the teeth, whereas parallel grinding and its concomitant rotation of the pharyngeal bones and pectoral girdle are almost absent (Figs. 10, 11). Skull rotation is only half as extensive as during grinding. Many cycles are intermediate between crushing and grinding.

4. Muscle activity patterns and movements

The interpretation of EMGs (Fig. 14) with movement data (Fig. 11) is based on the separate effects of the single muscle contractions (Fig. 7). However, because skull, branchial basket, and pectoral girdle have been proved to move, these effects are evaluated carefully. In addition the position of the pharyngeal bone itself changes continuously. In three experiments, the activity of the PCE, PCIP, and ROPI muscles were recorded bilaterally; occasional differences in timing of at most 20–30 msec were found. These differences are small in comparison with the long activity periods in

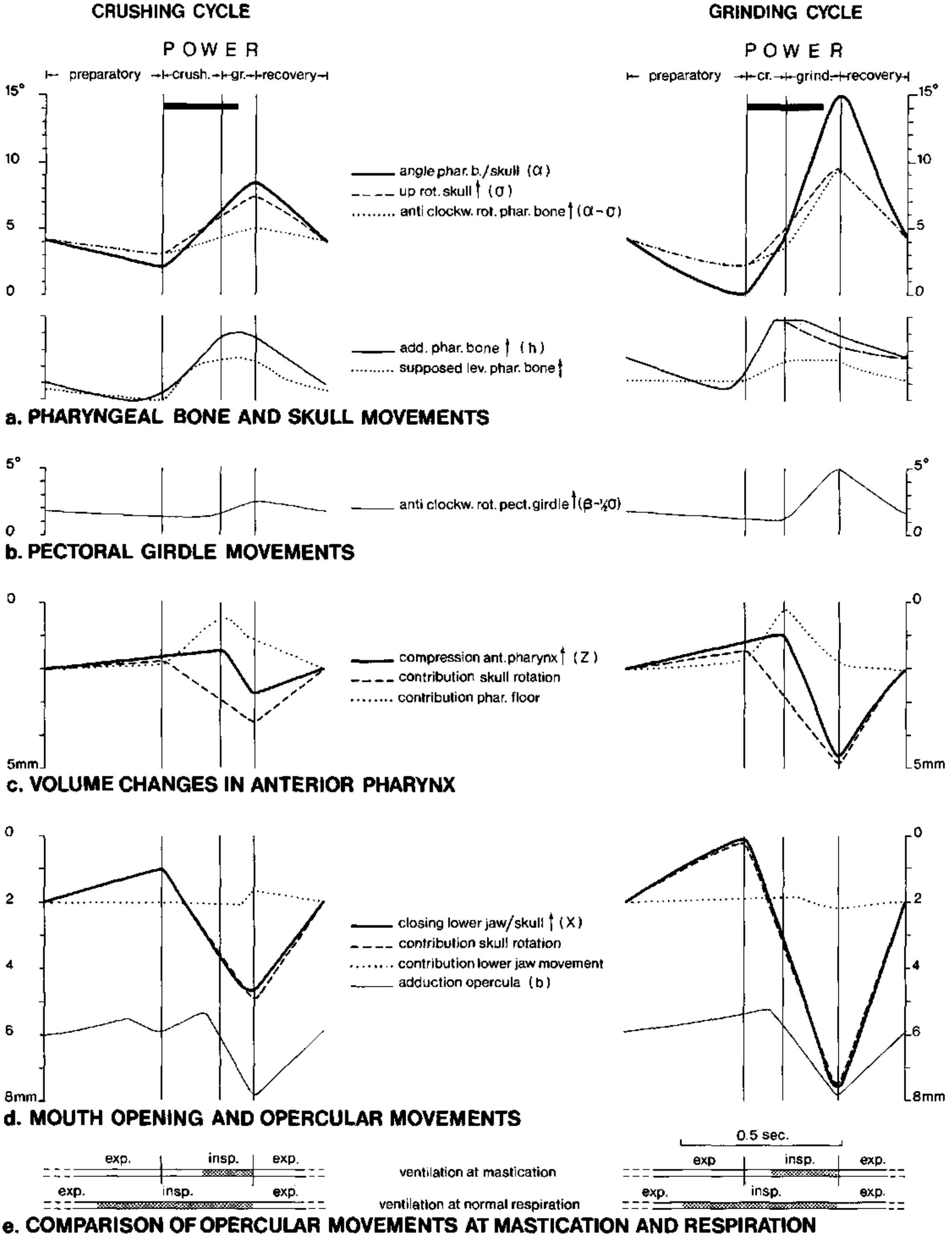
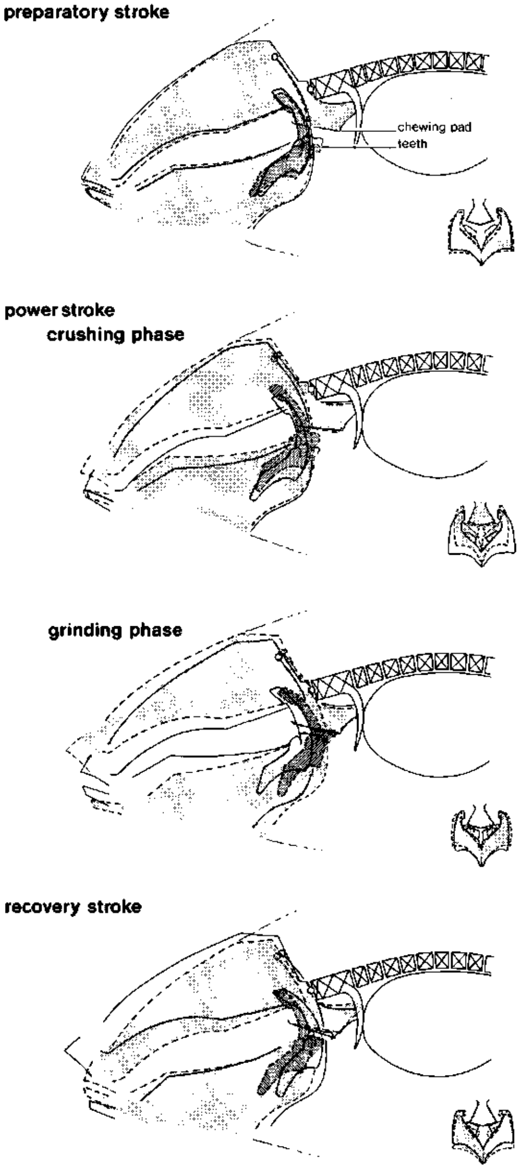


Fig. 11. Summarized data on the movement of head elements in crushing and grinding. The share of skull movements in the total effects is so essential, in providing masticatory power, that it is separately indicated. These data are visualized in Figure 12. The activity period of the LAB V muscle (black bar at the top) allows a comparison with the overall EMG pattern (Fig. 14). Consequences of masticatory movements for respiration (e) are inferred from the opercular movements during normal respiration (Ballintijn, '69b). Symbols as in Figure 8. For further explanation, see text. (Dorsad translation of the pharyngeal bones (a) is small and could not be measured free from other movement components. To complete this picture it is inferred from the LAB V activity.)


preparatory stroke

power stroke

crushing phase

grinding phase

recovery stroke

Fig. 12. A grinding cycle of the carp in lateral view, based on movement data of Figure 11 and X-ray images. Amplitudes exaggerated about 50% to show movements more clearly (such amplitudes probably do occur). The insets offer a half-sized rostral view on the pharyngeal bones and chewing pad to show adduction or abduction. For each of the four strokes, start (solid lines; white field) and final position (dashed lines; dark field) are indicated. The lines marking the pharyngeal lumen indicate bony parts; the actual lumen is, at the end of the preparatory stroke, fully occupied by the pharyngeal pad (cf. Fig. 4). Note the lifting of the pharyngeal floor and bones in the crushing phase, whereas the chewing pad remains in about the same position. In the grinding phase the teeth as well as the chewing pad move in opposite directions, wedging the food. Rotations of pharyngeal bones are distinct; pure retraction is hardly noticed. Skull and pectoral girdle movements contribute conspicuously to grinding; the pharyngeal lumen is extensively expanded. The picture of a crushing cycle differs by domination of the crushing phase over the grinding phase.

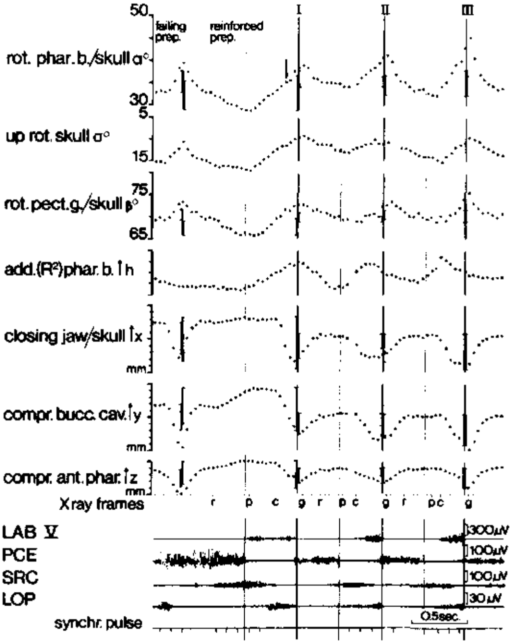


Fig. 13. Movements and EMGs during a failing crushing action and the subsequent repair activity. The terminations of the preparatory (p), crushing (c), grinding (g), and recovery strokes (r) are marked. Cycle I is a crushing, cycle III a grinding cycle with conspicuous pharyngeal bone abduction in the power stroke. The carp initially fails to bring a large food pellet between teeth and chewing pad (X-ray movie). This reveals, by accident, some of the regulatory mechanism (see text). Note that the skull rotates as if crushing were to follow, but that activity in the LAB V and SRC, and adduction of the pharyngeal bones, are omitted. Subsequently, the PCE and SRC muscles intensify the preparatory stroke, the buccopharynx is extremely compressed, and food is allowed to the teeth. In this first crushing cycle the pellet is broken into pieces (arrow). Vertical lines as in Figure 10. Symbols correspond to Figure 8a.

mastication.

Grinding cycle. Clockwise rotation (R^1) as well as protraction of the pharyngeal bones in the *preparatory stroke* is caused by activity in the PCE and SRC muscles (Fig. 10); the PCE also abducts (R^2 and R^3) the pharyngeal bones. The protraction is supported by activity in the muscular chain adductor mandibulae (A_2A_3)-protractor hyoideus (PRH)-sternohyoideus (STH) (Fig. 14) in the pharyngeal floor, which protracts the hyoid and the pectoral girdle and moves the pharyngeal floor to the food and the lowered base of the skull. The PCIA and PCIP muscles cooperate in these actions. Activity in the posterior pharyngeal roof (Fig. 9) will aid in the manipulation and transport of food caudad into the expanding posterior pharynx. The depression of the skull is mainly effected by activities in the A_2A_3 and probably also by other

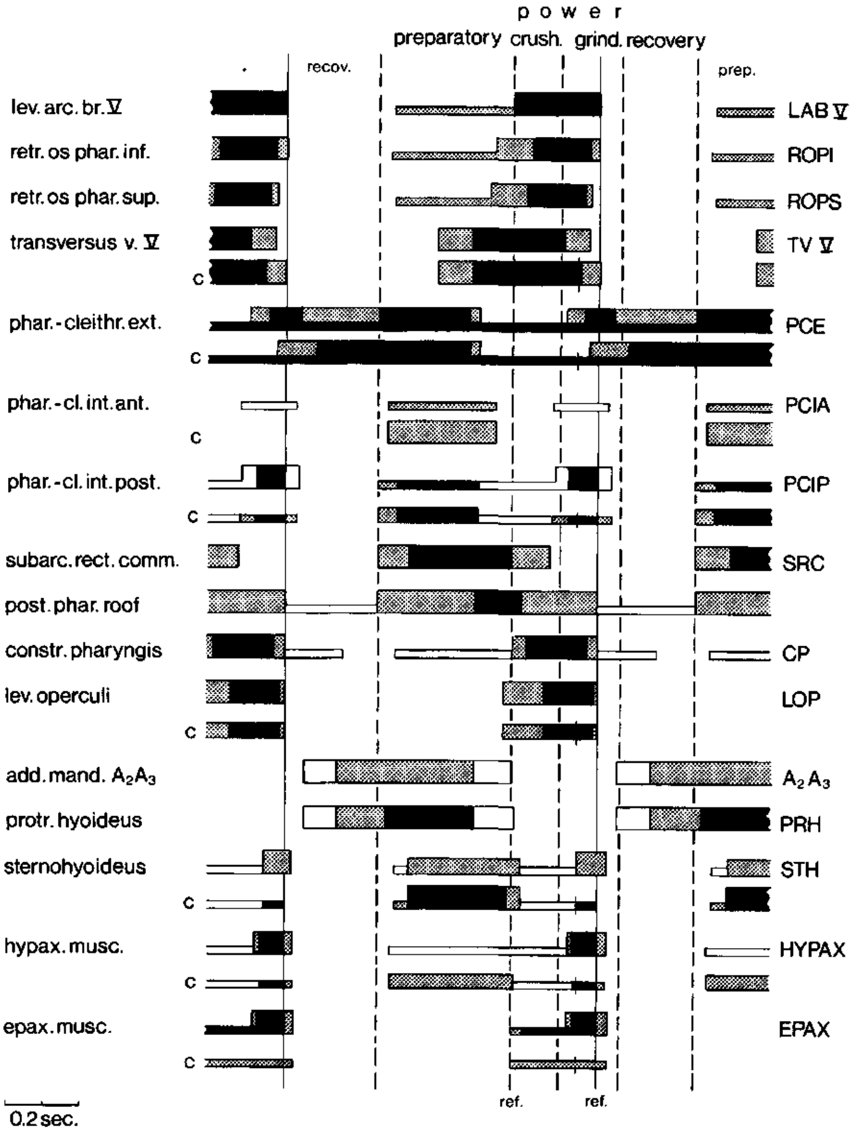


Fig. 14. Typical activity pattern of pharyngeal bone, head, and body muscles during a grinding cycle as computed from more than 30 experiments, each with numerous masticatory sequences. Where the activity in crushing cycles (c) is different from grinding cycles, this is indicated. Timing of the activity periods was related to the limits of LAB V activity (ref.). Three intensity levels are distinguished by the height of the blocks. Black bars indicate regular activity (>67%), dotted bars frequent (67–33%), and open bars occasional or maximal activities (<33%). Subdivision of the grinding cycle is extrapolated from simultaneous movements. The transition from the crushing phase into the grinding phase during the crushing cycle is marked by thin vertical bars. Note the sustained activity of the PCE in the powerstroke; this muscle balances the activities of multiple masticatory muscles.

head muscles compressing the buccopharynx. At the end of the preparatory stroke, the activity in the PCE decreases in favor of the antagonistic TV V muscle (Fig. 18); this results in adduction of the pharyngeal bones and in a more functional dorsad, instead of mediad, pointing of the crushing A I and other teeth. Considerable variation in the presence and timing of low activity periods was observed.

During the *power stroke* nearly all muscles are highly active. First, during the *crushing phase*, the pharyngeal bones are lifted by the LAB V and to a lesser extent by the CP muscles. This crushing movement is extended and powered by moderate activity of the epaxial muscles (EPAX) that lift the skull. Thereby, also the origin of the LAB V is lifted but not the chewing pad, because this pad lies close to and directly ventral of R^v. In addition the LAB V, ROPI and CP muscles rotate (R^1) the pharyngeal bones slightly anticlockwise. Increasing retraction components of the ROPI are initially counteracted by the SRC, ensuring occlusion of the A I teeth at the anterior zone of the chewing pad (see Fig. 2b, the impressions of the A I teeth). The posterior part of the pharyngeal roof (Fig. 9) acts in fixing the food in front of the teeth (Fig. 17b; frames 422–441) and in preventing the escape of crushed bits to the anterior pharynx. Both TV V, ROPI, and ROPS and probably the obliquus posterior muscles (not measured) strongly adduct (R^2 and R^3) the pharyngeal bones and thus support the crushing. The PCE muscles remain active throughout the power stroke though the amplitude is reduced (Fig. 9) and they oppose lifting, rotation, and adduction movements of the pharyngeal bones.

During the *grinding phase* of the power stroke, the LAB V and CP remain active; the activity in the EPAX increases, thus maintaining a strong lifting force on the skull and pharyngeal teeth. When the activity in the SRC ceases, the retraction components of the ROPI predominate and the dorsal processes of the pharyngeal bones abut and then rotate against Baudelot's ligaments between skull and pectoral girdle. Thus a new rotation axis R^4 is created (see ROPI in Fig. 7). The LAB V and ROPS muscles maintain the dorsal tips of the pharyngeal bones against the ligaments. This rotation around R^4 is intensified by activity of the PCIP muscles, which apply the pharyngeal bones as levers, and it is facilitated by depression of the pharyngeal floor by the STH and occasionally the PCIA muscles (Figs. 14, 15). The caudodorsad grinding movements of the teeth oppose the rostroventrad rotating chewing pad (Fig. 12) and are powered by the hypaxial body muscles (HYPAX; see Fig. 9). The latter retract the pectoral girdle and thus transmit their force through the PCIP to the pharyngeal bones and teeth. A shift in activity from the TV V to the PCE muscles (Fig. 18) and the sliding of the dorsal processes laterad along Baudelot's ligaments (see Fig. 7, action PCIP) may well cause abduction of the pharyngeal bones. This lengthens the grinding stroke of the teeth, as shown by the abrasion facets on the chewing pad (Fig. 2b). Adducting components of the ROPI, ROPS, and CP muscles in the grinding phase counteract this effect. In contradistinction to the name and to the common opinion, the main function of the ROPI is adducting the pharyngeal bones (crushing phase) and rotating them, owing to the presence of Baudelot's ligaments (grinding phase). Pure retraction of the dorsal tips has hardly been measured during mastication (cf. Sibbing, '76: Fig. 1).

Termination of activity in most masticatory muscles indicates the start of the *recovery stroke* (Fig. 14), but some muscles (PCIA, PCIP, STH, HYPAX, EPAX) may continue to be active for another 20–30 msec. The rotation of the skull and pharyngeal bones lasts even longer (Fig. 10), owing to a delay between the action potentials measured and the resulting tension or mechanical output in the construction. This is discussed later. Return of the pharyngeal bones during the recovery stroke to an intermediate position that permits reorientation or transport of food is effected by the PCE that acts as a key antagonist and by the elastic recoil in muscles and ligaments. The return is accompanied by protraction of the pectoral girdle and depression of the skull. Apart from the A_2A_3 and PRH, other adductors in the buccal and pharyngeal walls will participate in these effects, but these have not been investigated.

Crushing cycle. The movement and EMG profile of the crushing cycle can easily be derived from the grinding cycle, through an extension of the crushing phase and shortening the grinding phase (Figs. 10, 11, 14). During mastication of hard maize, the crushing by the fish can even be heard. Lifting of the pharyngeal bones in the crushing phase is preceded by powerful protraction of the hyoid and pectoral girdle and compression of the anterior pharynx (A_2A_3-PRH-STH, and PCIP-PCIA) in the preparatory stroke (Fig. 13, cycle I; Fig. 14). This mechanism also expands the posterior

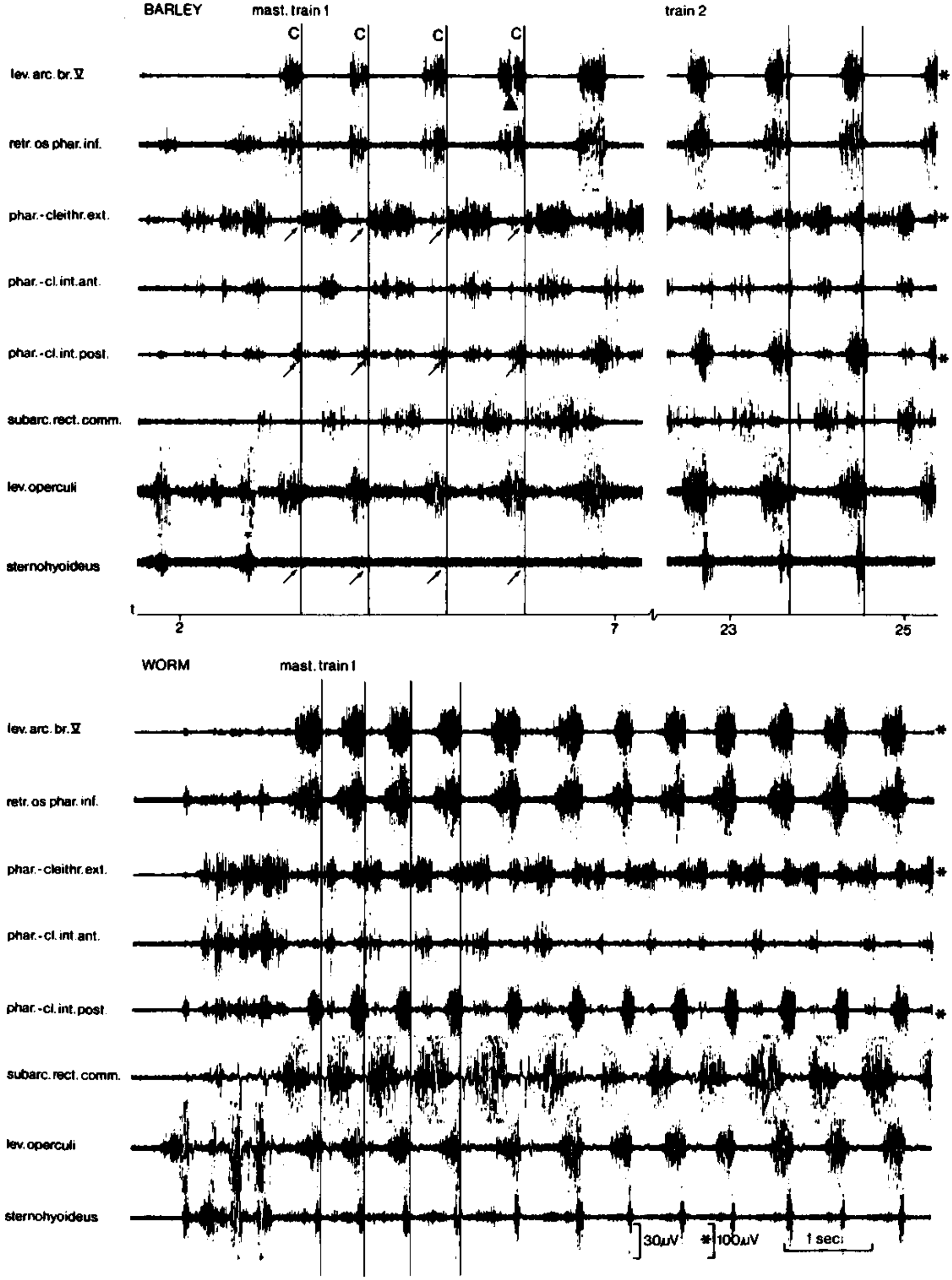


Fig. 15. In contrast to the mastication of worms, mastication of barley starts, in the same experiment, with a series of crushing cycles (c); these lack high activity in the PCIP, STH, and PCE muscles in the power stroke (arrows) and show increased PCIA activity in the preparatory stroke. Activity patterns in grinding worms or barley are similar. The short interruptions in the LAB V and ROPI activities (see ▲) probably reflect momentary adjustments to the food. Note the repetitive activity in the LOP and pharyngeal floor muscles (PCE, PCIA, PCIP, STH), prior to the first masticatory cycle of worm and accompanying the transport of food to the teeth.

pharynx widely and thus allows the passage of large particles between teeth and chewing pad. Adduction of the pharyngeal bones (R^2 and R^3) is as extensive as during grinding, but abduction scarcely occurs in the power stroke; this explains the sustained TV V activity and the lack of high activity in the PCE and PCIP in the power stroke (Figs. 14, 15). During the grinding phase of the crushing cycle, rotation of the pharyngeal bones around Baudelot's ligaments (R^4) hardly occurs; this agrees with the absence of high PCIP activity. In addition, the retraction of the pectoral girdle (HYPAX), depression of the pharyngeal floor (STH and PCIA), lifting of the skull (EPAX), and consequently expansion of the anterior pharynx are only small in the crushing cycle (Fig. 11).

During the preparatory stroke of the crushing cycle, the STH and PCIP muscles can act as protractors of the pectoral girdle, because the jaws are adducted and the hyoid arch and pharyngeal bones are protracted. In the power stroke of the grinding cycle, these muscles act as retractors of the hyoids and depressors of the pharyngeal floor, as the pectoral girdle is retracted.

A time lag occurs between the end of electrical activity and the peak of mechanical events (e.g., pharyngeal bone/skull rotation in Figs. 10, 11). Møller ('66), and Ahlgren and Öwall ('70) reported 100 msec for such a lag during mastication in man. Desmedt ('58) observed that muscular tonus lasts 150 msec longer than electrical activity. Inman et al. ('52) found a value of 80 ± 20 msec, and Hannam et al. ('75) 73 ± 12 msec for the delay in man between the peak of electrical activity and the peak of muscular tension. The value measured for mastication in the carp, a time lag of 40–80 msec, fits these data. Because masticatory cycles commonly last between 600 and 900 msec, this delay does not affect the interpretation of the EMGs by more than other factors, such as elastic recoil.

5. EMG variations in the course of mastication

As the particle size and consistency of the food change continuously during mastication, adjustments in the processing of food are expected.

Crushing precedes grinding in a masticatory sequence (Figs. 9, 10, 13, 15) as well as within the individual cycle. Many cycles with an intermediate profile occur. Crushing is far less frequent and even absent during mastication of soft food (Fig. 15), whereas grinding is common.

During the early part of a masticatory train, much power is needed. Masticatory cycles are short and muscles are highly active (Fig. 9). Muscles that contract in the preparatory stroke may already be active in the recovery stroke. In the course of the masticatory sequence the activity diminishes to an intermediate level (shown in Fig. 14) characterized by continuous activity in the PCE only. Finally the activity of the PCE between successive power strokes breaks up and a masticatory pause is interposed (Fig. 9). Overall reduction of the activity level is seen in this final part of the masticatory sequence, accompanied by the more frequent occurrence of isolated cycles and masticatory pauses. Only periods of activity with high amplitudes in the early phase of mastication are still observed. This probably reflects the diminished force in the individual cycle and the smaller velocities of movement, as the desired particle size is attained.

6. The influence of the type of food on mastication

Feeding various foods in the same experiment produced different EMGs (Fig. 15), and it further justified the distinction of crushing and grinding cycles. Mastication of soft worms requires only grinding cycles with activity of the PCIP, PCIA, STH, and HYPAX muscles in the power stroke. If hard and compact barley is fed, grinding cycles are preceded by crushing cycles, without the activity of these specific muscles. The grinding cycles after feeding of worms and barley are similar and correspond to the typical pattern. Fewer cycles are observed in mastication of soft worms, compared with hard barley, which may cause mastication to last for minutes. No detailed knowledge exists about the sensory system that detects the differences in food consistency.

7. Mastication and respiration

Mastication incorporates the respiratory movements. This is concluded from a comparison of the opening of the mouth, the volume changes in the buccopharyngeal cavities, the abduction of the opercula, and the activities in the LOP and pharyngeal floor muscles during mastication and normal respiration (Figs. 11, 16). Expiration coincides with the recovery and preparatory strokes and even continues in the crushing phase of the power stroke; this is inferred from the pharyngeal compression and opercular adduction (Fig. 11c,d,e) (Ballintijn, '69a). Inspiration coincides with the remainder of the power stroke. The duration of the masticatory and the normal respiratory cycle lie in the same range (about 0.8 second). Compared with normal respiration, the inspiratory phase during mastication is halved, and the expiratory phase is doubled (Fig. 11e). The kinetics of mastication dominate respiration (compare Figs. 10, 16).

These data are explained by the structural as well as the functional coupling between respiration and mastication. The extensive rotations of the pharyngeal bones during mastication, especially in grinding, can only be realized through concomitant movement of the pharyngeal floor. This movement triggers the volume changes in the buccopharyngeal and opercular cavities that are larger than in normal respiration (Fig. 16). The functional coupling between mastication and respiration is also demonstrated by the activity in pharyngeal bone muscles during strong inspiration (ROPI often, LAB V frequently, and PCE-PCIP occasionally active), and by the activity of muscles that function in hyperventilation (Ballintijn, '69a) during the power (LOP, STH, HYPAX) and the preparatory strokes (A_2A_3-PRH-STH-TV IV) of mastication (cf. Fig. 17a).

During *quiet respiration* the fifth branchial or masticatory arch acts as an integrated part of the branchial basket and moves only slightly (Fig. 16). The pharyngeal bones perform no intrinsic movements. At *hyperventilation*, the pectoral girdle and hyoid arch are retracted, the pharyngeal floor is depressed, and pharyngeal bone rotation is more extensive. The skull rotates only slightly (1.5°) and plays a minor role in the large buccopharyngeal expansion. During *mastication* this expansion is equally large but results from the lifting of the skull (7°) rather than from lowering of the pharyngeal floor. The absence of activity in the EPAX and strong activity in the STH at hyperventilation fits in this picture. During mastication the pectoral girdle and pharyngeal bones rotate further; only then the bones perform adducting movements.

8. Food intake, transport, and deglutition

Transport of food to the teeth, documented by X-ray movies with radiopaque (barium sulfate impregnated) food pellets (Fig. 17), is subdivided into three distinct phases:

a. The rapid intake (50 cm/sec) by suction, which passes the food through the buccal cav-

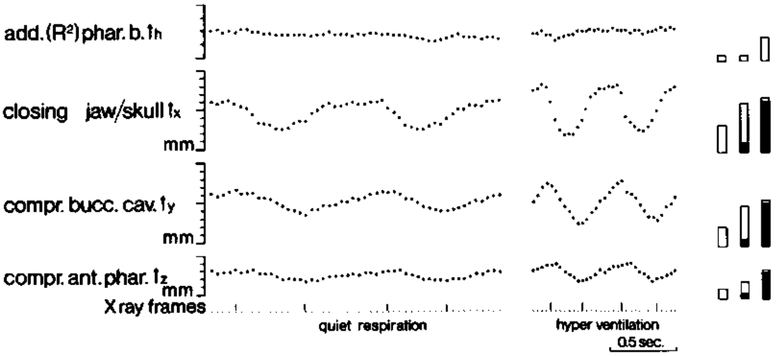


Fig. 16. Comparison of quiet respiration (R), hyperventilation (HV), and mastication (M). Symbols correspond to Figure 8a. Bars at the right aid in comparing the amplitudes; black parts indicate the share of the skull. Note the equally large expansion of the buccopharyngeal cavities, caused by floor movements in hyperventilation, and by skull movements mainly in mastication. The shape of these curves differs from those during mastication (cf. Fig. 10). Pharyngeal bone movements participate in hyperventilation. in, inspiration; ex, expiration.

ity until it is caught between the roof and floor of the anterior pharynx (Fig. 17; frames 15–20). The flow of water continues laterad through the branchial filter.

b. Further caudad, transport is effected by the peristaltic bulging of the pharyngeal pad (frames 81–115), observed in a freshly killed fish, and caused by repetitive activity in the pharyngeal roof (Fig. 9). The only area in the pharyngeal floor that is markedly muscular lies right in front of the teeth and cooperates in this propulsive action. Mucus produced by the pharyngeal epithelium reduces the transport resistance. During this second transport phase the pharyngeal floor often makes repetitive vertical movements and the transport of food occurs only stepwise, when the depressed pharyngeal floor is lifted (measured from X-ray movies). The simultaneous repetitive activity of the PCE and other pharyngeal floor muscles (Figs. 9, 15) and the clockwise rotation of the pharyngeal bones indicate that the posterior pharynx tends to expand. (Repetitive expansion of pharyngeal and opercular cavities prior to the food transport functions probably in cleaning the food, because waste particles appear from the opercular slits.) The food finally reaches the rostral margin of the chewing pad (see frame 115), wedged between the two muscular pads, and is stored there.

c. Usually food is propelled directly into the expanding posterior pharynx between teeth and chewing pad (see frames 232–272). This transport phase is continuous with the intensive preparatory stroke of the first masticatory cycle and effected by the same mechanism (cf. PCE activity in Fig. 17).

Food pellets that are too large to chew as a whole, are crushed first, then ground as separate bits (last cycle, frames 422–430) and transported into the esophagus (frames 436–441). The remainder of the pellet lies at the rostral margin of the chewing pad, or occasionally further rostral in the pharynx, where it is stored to be crushed later.

Masticatory trains are usually completed by some short masticatory cycle, in activity as well as in movement of low amplitude (Figs. 9, 10, 17). This typical pattern (Fig. 18) always coincides with food transport into the short vertical esophagus (compare Fig. 17; frames 436–441) and characterizes the *deglutition stroke*. Most distinct, in comparison with a crushing cycle of low amplitude, is the sustained high activity in the posterior part of the pharyngeal roof (Fig. 9) and the even higher activity in the constrictor pharyngis muscle (Fig. 18). Thus, deglutition of the ground and lubricated food probably results from contraction of the wall of the posterior pharynx, facilitated by a small concomitant movement of the pharyngeal bones. Activity in the constrictor pharyngis muscle might continue into the esophageal peristalsis. Escape of the food to the anterior pharynx is blocked by the bulging of the muscular pads in front of the chewing pad and the teeth. The deglutition stroke is commonly followed by the recovery activity of the PCE and a short masticatory pause; then another train is initiated, breaking off another

>scenes. b. X-ray cinerecording of the successive feeding ac -

Fig. 17. a. EMG record of the feeding process depicted in panel b (numbers refer to the X-ray frames). The activity patterns are characteristic for food intake, transport, and deglutition, as appears from Figure 17b and many other >tions in the carp (26 frames per second). Black markers correspond to Figure 8a. Feeding starts with rapid intake (50 cm/sec) of the radiopaque ($BaSO_4$-impregnated) food by suction. Note the expanding buccopharynx (frames 15–20). Later, the food is transported more slowly through the anterior pharynx to the rostral margin of the chewing pad (frames 81–115), and finally into the expanding posterior pharynx, between teeth and chewing pad (frames 232–272). The latter transport is continuous with the intensive preparatory stroke of the first masticatory cycle. After the last grinding cycle (frames 422–430) the masticatory train is completed by deglutition (frames 436–441) (see arrows). The remainder of the pellet stays at the rostral margin of the chewing pad.

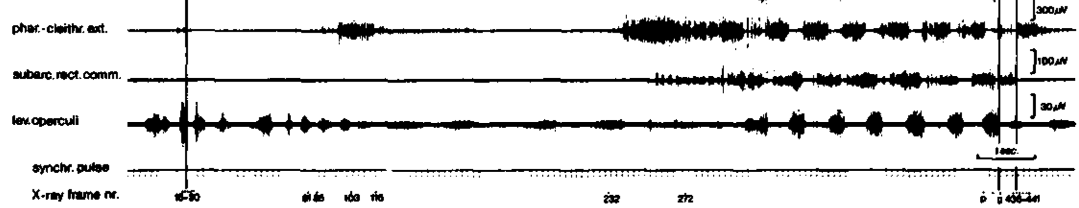


Figure 17a.

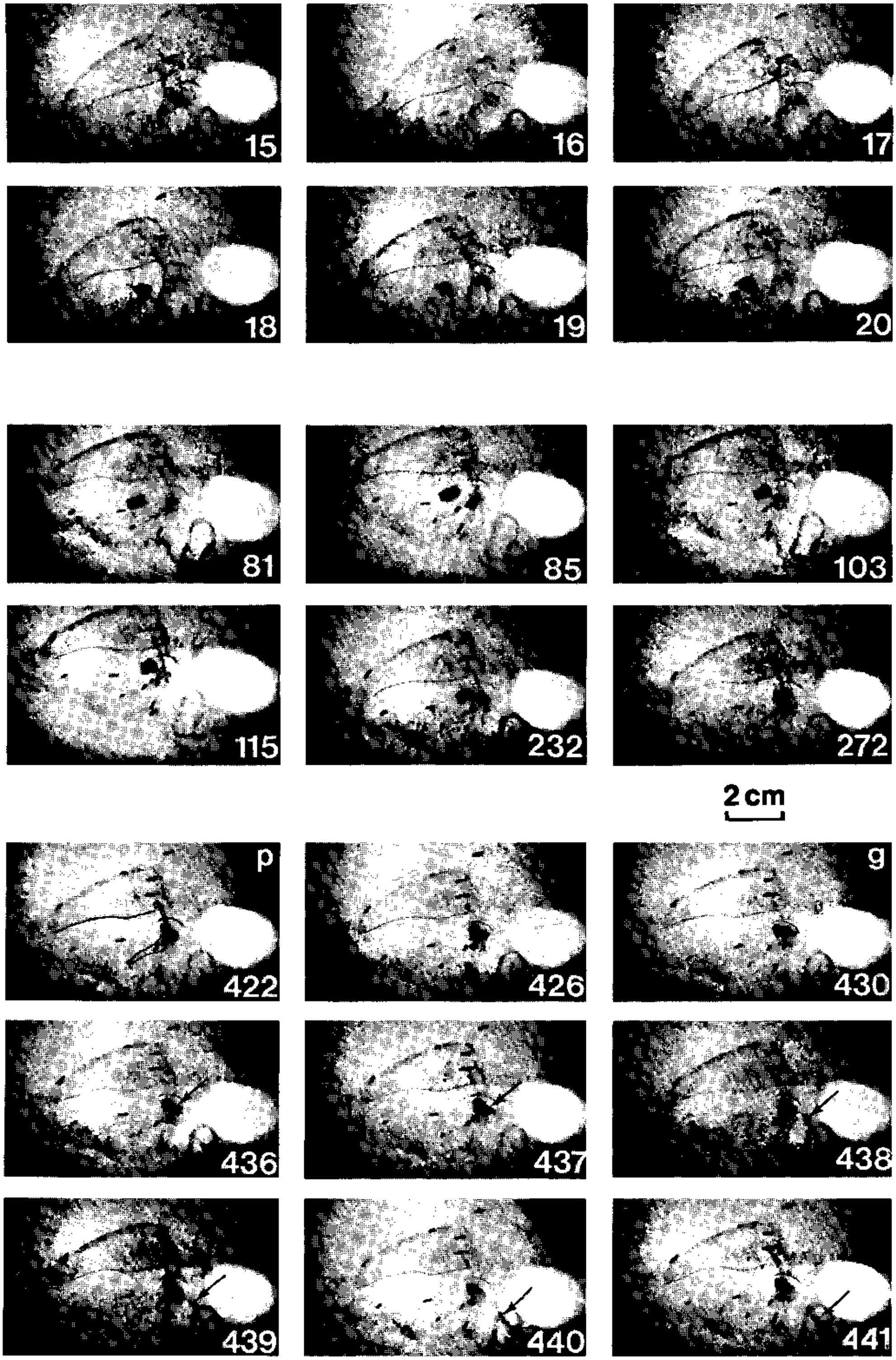

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Figure 17b.

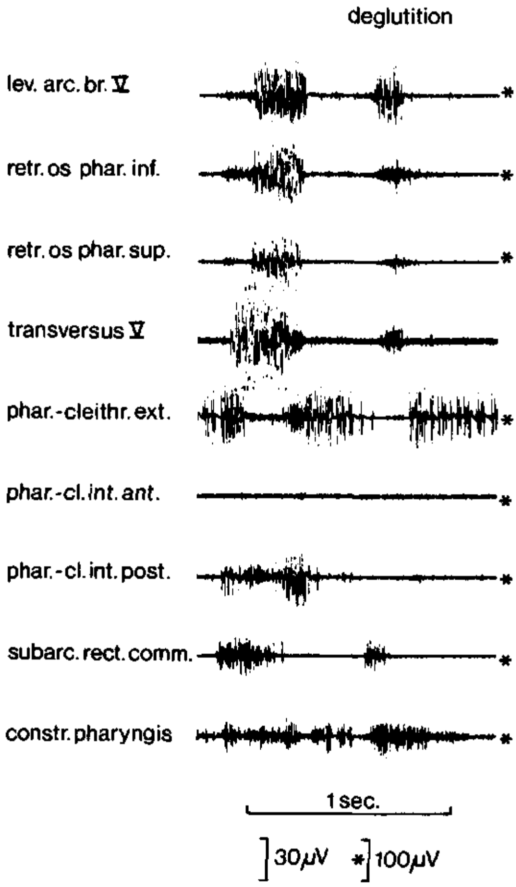

Fig. 18. Activity pattern of the pharyngeal bone muscles during deglutition, following a grinding series. Deglutition resembles a crushing cycle of low amplitude. Note, however, the sustained high activity in the PCE and the increased activity in the constrictor pharyngis muscle.

piece. Occasionally the masticatory pause lasts longer and repetitive activity is observed that resembles the pattern after initial suction of the food. This indicates that food, stored in the anterior pharynx, is transported towards the chewing pad.

DISCUSSION

The primary functions of a masticatory apparatus are to reduce the particle size of the food, in order to expose a larger area to the digestive enzymes, and to reach nutritive materials contained within hard or indigestible shells. The masticatory apparatus is also involved in mixing, lubricating, and transporting food. Its supporting role in respiration is discussed.

The masticatory effect depends mainly on the hardness, the profiles, and the relative movements of the occlusal surfaces, and on the properties of the food. A multiplicity of terms is used to characterize the masticatory process (tear, crush, grind, grasp, mince, lacerate, cut, penetrate, shear, puncture, triturate). Definitions, however, are mostly insufficient or even lacking. Therefore, some principal operations are defined below and, in advance, terms that describe material properties are outlined briefly.

Definitions of masticatory terms

The profile of the occlusal surfaces and the direction of their relative movement determine the type of load: compression, tension, sliding, bending, or torsion. Materials are unequally resistant to the different loads; qualifications as hard and soft indicate the amount of stress that a material can bear before fracturing, but they require load specification. If the strain at a given stress is high, the material is *elastic*; if it is low the material is *stiff*. When it yields extensively before fracturing it is *tough*; otherwise it is known as *brittle*. The high strain that elastic and tough materials require for fracturing demands extensive excursions in the comminuting machinery.

Material properties of natural foods have never been specified and the properties of composite materials cannot simply be deduced from the separate components. Therefore, only a rough deductive approach can be made to the relation between the masticatory construction and food properties.

Masticatory operations

In accordance with Rensberger ('73) four masticatory operations are distinguished (Fig. 19):

Crushing. One or both parallel smooth areas approach at right angles to their surfaces. Compression is the main load. Stresses are inversely related to the area of contact. Crushing is applied to stiff and brittle materials of different hardness and shape.

Cutting. One or both parallel areas, one smooth and the other provided with ridges, approach at right angles to their surfaces. Compression is the main load. Stresses are high because of the small area of contact. The deformation capacity is proportional to the height of the ridges. Cutting is applied to hard materials of moderate elasticity and toughness.

Shearing. One or both parallel areas, each provided with ridges, approach at right angles

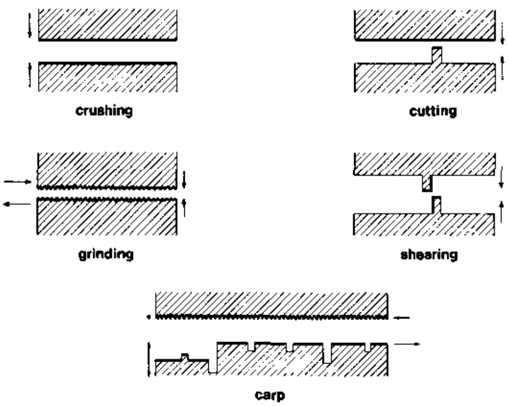

Fig. 19. Four types of diminution, distinguished by the occlusal profiles and their movements (arrows). They involve different loads (see text). At the bottom the occlusal system of the carp is schematized. Note the structural and functional ability to crush and grind in the carp, and the inability to shear.

to their surfaces. Opposite ridges closely pass each other and effect compression, sliding, and tension. Owing to the very small area of contact, stresses are extremely high. Deformation capacity is large and proportional to the summarized height of the ridges. Shearing is applied to hard, elastic, and tough materials.

Grinding. One or both contacting rough areas move parallel to each other. Sliding and tension are the main loads. Compressive stresses are moderate, owing to the numerous but small areas of contact, and they play a secondary role. Contacts change continuously; the deformation capacity is high and proportional to the extent of parallel movement. Grinding is applied to soft, elastic, tough, and fibrous materials or to a multiplicity of small particles of varied consistency.

The almost continuous variation in cyprinid pharyngeal teeth and the varied masticatory operations that will be performed illustrate that the above distinction, in four types, is but a first approach. A further differentiation has to be made in a future comparative study.

Occlusal surfaces and types of food

In the occlusal surfaces of the carp and their movements, both crushing and grinding operations are evident (Fig. 19). There is no ability for cutting and shearing, owing to the extensive contact with the smooth chewing pad; teeth on both sides do not interdigitate.

Furrows in the occlusal surfaces and the open areas between adjacent teeth permit extensive deformation, provide a firmer grip on the food, and improve fracturing. The sinuous shape of the furrows, and their orientation at right angles to the direction of grinding (Fig. 2b), improve grip during transport. The enlargement of successive generations of crowns, from young to old carps, is not accompanied by an increase of grip-distance between furrows but by a larger number of furrows and it does not affect the masticatory operations. The pointed center in the crown of the A I teeth acts as a chisel for brittle materials and punctures tougher material prior to crushing (see Results). Few authors attribute a role in mastication to the A I teeth, because they are distant from the chewing pad and largely covered by mucosal folds. These teeth function, however, in the vertical movements and crush large particles. Besides, the mucosa has been proved to contract during the power stroke.

The flat chewing pad is essential in both crushing and grinding. Its horny substance is not so hard and is more easily eroded than the dentine of the teeth; the chewing pad, however, is renewed continuously by the epithelium (Eastman, '70). The grinding path on the chewing pad runs caudolaterad and the effective stroke is almost twice as large as the crowns (Fig. 2b). Large and stiff food objects are bent and fractured by compression at both sides of the medial ridge. The chewing pad previously was assumed to be motionless; it moves, however, with the skull. Its small but powerful rostroventrad movement is opposite to that of the teeth and intensifies grinding considerably.

Analysis of occlusion, intestinal contents, and feces shows that comminution of arthropods, molluscs, and seeds occurs mainly by crushing, followed by grinding the interior parts. Fibrous and tough higher plants are wedged between teeth and chewing pad; the numerous local and continuously changing contacts during grinding disrupt the texture and wash out the cells. Sand grains that are frequently present in the occlusal furrows aid this action. Elastic food such as worms is largely resistant to crushing and grinding. Puncturing by the A I teeth allows penetration of digestive enzymes. It is highly probable that proteolytic enzymes in the crushed cells of invertebrates aid in digestion by autolysis (Dabrowski and Glogowski, '77).

The position of the crushing A I teeth, anterior to the grinding teeth, and the timing of the crushing movement, prior to grinding in the masticatory series and within the individual cycle, assure a gross reduction by crushing prior to the finer reduction by grinding. In technology, different types of machinery are used for diminution of diverse materials and even for unequally sized particles of a single material. The heterodont carp is provided with a masticatory apparatus that integrates crushing, grinding, and puncturing, and fits the omnivorous feeding habits. The apparatus evidently is specialized for polyphagy.

Effective mastication in the larval fish depends on the development of the anatomical features and is only possible from the 20th day after hatching (Geyer, '37). Subsequently, the diet changes and successive generations of differently shaped teeth occur (Vasnecov, '39). The final shape, as described here, is attained only after 10 months. Examination of the extent to which changes in the diet and in the occlusal morphology, the latter being partly determined by the evolutionary history of the species, are functionally coupled is in process.

There remains the important question: To which degree is diminution required for efficient feeding? It has been shown that the lack of a stomach in cyprinids does not affect the capability for digestion, at least of proteins (Shcherbina et al., '76; Stroband et al., '81).

Structural and functional design of the masticatory construction

Mastication depends on the mechanism that drives the occlusal surfaces. A discussion of the force, direction, and extent of the occlusal movements, and an examination of the construction driving them, will extend the analysis of form and function to the apparatus as a whole.

Crushing

Forces at right angles to the chewing pad are essential in all masticatory operations. They predominate in crushing and are imposed mainly through lifting of the pharyngeal bones, partly by the LAB V and partly by the EPAX muscles (Fig. 20). The transmission of forces from the body muscles to the pharyngeal bones and teeth explains the conspicuous aponeurosis in the interposed LAB V muscle (Fig. 5).

Initially, the LAB V and EPAX contract and effect a powerful acceleration of the teeth at right angles to the chewing pad. Following the length-tension diagram, production of forces in the LAB V will decrease if it shortens. Lifting of the pharyngeal bone is blocked by occlusion at the end of crushing. Continued lifting of the LAB V origin with the skull prevents shortening and must even stretch the LAB V, bringing it again to its resting length and thereby increasing force production. Owing to the tendinous elements in this muscle, passive tensions get increasingly higher during the grinding phase and forces imposed on the food are maximal. Hill ('70) found that the tension produced by stretching an active toad muscle, during a tetanus, was substantially higher than the maximum isometric tension at the stretched length. If this applies to the LAB V, forces on the food are even higher than already argued. The skull provides an extensive origin for the LAB V, which has a 33% share in the total wet weight of pharyngeal bone muscles and a large moment with respect to R^1. The high skull provides an effective lever, and the medial supraoccipital crista extends the insertion area for the epaxial muscles. A similar device on the supraoccipital is observed in predatory mammals that use their nuchal muscles in tearing pieces off their prey. The mentioned characters make the LAB V-EPAX combination an effective and unique power-providing system in mastication.

Crushing power is further added by adduction (R^2 in Fig. 7) of the pharyngeal bones by the ROPI, ROPS, and to a lesser extent the TV V muscles, which turn the dorsomediad facing occlusal surfaces dorsad. Teeth movements are small, owing to their position close to the R^2 axis, but they increase the imposed force.

Grinding

Forces parallel to the chewing pad, essential in grinding, are provided by the ROPI, PCIP, and the body muscles. Compressive forces are maintained during grinding by the lifting and adduction of the pharyngeal bones, as discussed above.

Parallel forces are exerted as soon as retraction of the pharyngeal bones is obstructed by Baudelot's ligaments. These ligaments were never before mentioned in relation to mastication, but they play a crucial role by forcing the bones into rotation (R^4; Fig. 7). Owing to the position of the teeth ventral to R^4, their movement changes from at right angles to the chewing pad in the crushing phase (around R^1) into parallel to this pad (around R^4) in the grinding phase. Because the teeth lie close to the fulcrum their excursion is reduced but the applied force amplified. (Owing to the muscular suspension of the pharyngeal bones, a large food particle may well be the instantaneous center of rotation.) The ROPI and PCIP muscles are the main instigators of the rotation around

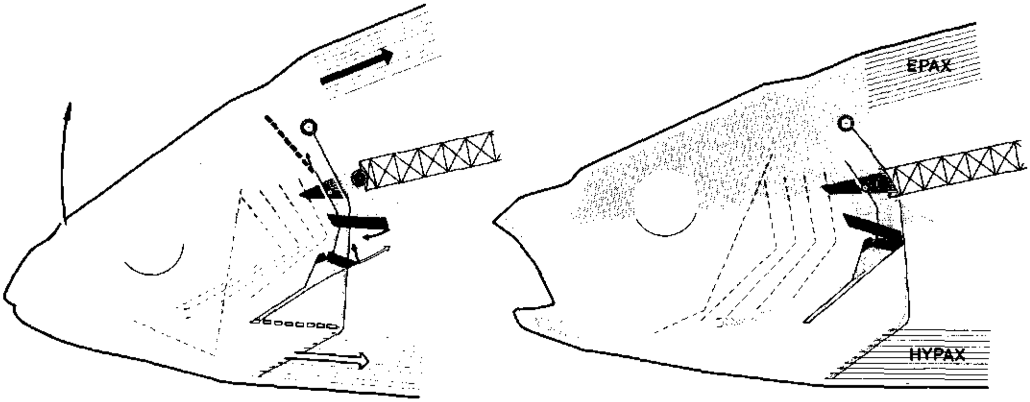

Fig. 20. The body muscles of the carp provide the power in crushing and grinding (indirect masticatory muscles). Epaxial muscles rotate the skull effectively dorsad, and thereby lift the pharyngeal bones and teeth to the chewing pad through the interposed tendinous LAB V muscles (heavy dotted). The pad itself is not lifted and moves mainly rostrad. (Black center of rotation, black arrows.) The hypaxial muscles retract the pectoral girdle effectively. Their forces are transmitted to the pharyngeal bones and teeth by the tendinous PCIP muscles and are added in grinding. The ligament between skull and pectoral girdle obstructs pharyngeal bone retraction dorsally, acts as a fulcrum, and effects rotation with the bones as long levers. (Open centers of rotation, open arrows). As a combined result, teeth and chewing pad move parallel, but in opposite directions, and wedge the food under high compression. Grinding movements are small but powerful. The extensive movements of the pharyngeal bones are permitted by simultaneous expansion of the buccopharynx and a slide-coupling in the branchial floor. Direct masticatory muscles that suspend the pharyngeal bones in muscular slings and steer these movements are omitted in this scheme.

Baudelot's ligament (R^4). The PCIP muscles apply the horizontal limb of the pharyngeal bone as lever and these limbs extend ventrad even under the basibranchials. The effect of PCIP action is greatly extended in force and amplitude by the powerful hypaxial body muscles that most effectively retract the pectoral girdle (Fig. 20) and thereby the origins of the PCIP muscles. The medial part of the PCIP is even continuous with the HYPAX. The transmission of body power to the pharyngeal bone and teeth is reflected in the massive PCIP tendon (Fig. 5) and in the extensive cross section at the origin on the cleithrum; this is analogous to the role and architecture of the LAB V (see above).

The excessive rotation of the pharyngeal bones is allowed by the slide-coupling between basibranchial III and the anterior cartilage (Figs. 5, 20) and is supported by concomitant depression and retraction (PCIA, STH, HYPAX) of the pharyngeal floor. Gosline ('77) supposes the cleithra in cyprinids to be relatively motionless; these data prove that they rotate (8°) with respect to the skull. These results also exemplify the idea of Nelson ('69) that the consistent division in the basibranchial series between the third basibranchial and the posterior copula in lower teleosts increases the potential of lower pharyngeal bone mobility.

Rotations around R^2 and R^3 add forces parallel to the chewing pad; initially these act mediad (ROPI, ROPS, TV V, and OP) but, as grinding proceeds, more laterad. The caudolaterad sliding of the dorsal processes along Baudelot's ligaments guides the pharyngeal bones into abduction (Fig. 7), especially by action of the PCIP; this lengthens the effective stroke. Retraction of the lateral attachments of these ligaments with the pectoral girdle cooperates in generating this abduction.

The epaxial muscles rotate the posterior part of the chewing pad increasingly rostroventrad (Fig. 20); in combination with the opposite teeth movements this intensifies sliding and compression in grinding.

It is evident that the design of the masticatory apparatus favors the transmission of forces of the dorsal and ventral body muscles to the small contact areas between food, teeth, and chewing pad. The pharyngeal bone muscles in the carp steer the masticatory movements and adjust the application of forces.

Analysis of the anatomical data is basic in defining the action of the pharyngeal bone muscles (Fig. 7), but their role in mastication appears only from a functional analysis. The concert of pharyngeal bone, skull, and pectoral girdle movements affects the lines of action and the range of movements. Besides, axes of rotation may shift. Moments of the PCIP and TV V muscles, for example, increase during the motion they aid to perform. The STH muscles act as protractors in the preparatory stroke and as retractors during the grinding stroke. Furthermore, the ROPI muscles rather rotate and adduct the pharyngeal bones, more than their name would suggest. The PCIP appears to be one of the major, though indirect, abductors. The ROPS and TV V muscles play a concealed role in stabilizing the masticatory movements.

Suspension and structure of the pharyngeal bone

The pharyngeal bones are suspended from the skull in muscular slings (Kallen and Gans, '72; Liem, '78) held in constant tension by some of the muscles (e.g., the PCE in Fig. 9). Combined with a movable symphysis and a slide-coupling in the pharyngeal floor, this suspension permits highly versatile and complex movements. The LAB V, ROPI, PCIP, PCE, and SRC muscles control the pharyngeal bone movements in the sagittal plane, whereas the LAB V, ROPI, TV V, PCE, and OP muscles cooperate in the transversal plane. The essential role of the ROPI in each of these systems may account for the unique presence of such retractores in cyprinids among lower teleosts (Holstvoogd, '65; Rosen, '73).

In the grinding phase Baudelot's ligament acts as a fulcrum and the pharyngeal bone is applied as lever. The pharyngeal bones provide areas of insertion and rotation axes at such sites that muscles form effective rotation couples. This renders the shape of the pharyngeal bone suited to accumulate power in mastication. Thus the LAB V, ROPI, and PCIP muscles, for example, although having completely different positions and lines of action, all contribute to rotation (R^4) of the bones in the grinding stroke. Because teeth are close to the R^2 and R^4 axes during grinding their movement is small but forceful.

The direction of the trabeculae in bony elements will reflect the direction of loading (Kummer, '62). The orientation of the distinct trabeculae in the basioccipital process suggests that they spread forces, imposed on the chewing pad, over the base of the skull and the exoccipitals and thus reduce excessive local stresses. In a similar way the trabeculae radiating from the toothed center of the pharyngeal bone (Fig. 2a), as well as the anterior limb extending rostroventrad from the A I teeth, spread reaction forces on the occlusal surfaces of the teeth over the bone. The angle of about 65° between the anterior limb and the occlusal surfaces of the teeth may well be a compromise in absorbing loads varying between perpendicular and parallel to the occlusal surfaces.

The free suspension of the pharyngeal bones raises the need for stabilizing the powerful movements. Muscles act bilaterally and antagonistic muscles are synchronously active. A disturbed balance in the movement and load of left and right pharyngeal bone, induced by irregularities of the food, will be corrected by the adjustments in the muscular sling (e.g., ROPI and LAB V against PCE in Fig. 15). Such an unbalance loads the symphysis mainly by sliding. Because the interpharyngeal ligaments lie almost parallel to the longitudinal axis (Fig. 6, max. 30°), they provide more resistance to such sliding load than to tensile forces bringing the pharyngeal bones apart. Rotation around the R^2 and R^3 axes (Fig. 3) causes compression and tension in the symphysis; these stresses will be absorbed by the symphyseal tissue. Owing to the movable symphysis, torsion of the bones will hardly occur. Excessive rotations around R^2 and R^3 are prevented by the interpharyngeal ligaments, by TV V activity, and by the closely joined, flat medial sides of the symphysis, which abut at large rotations. Some other muscles may aid in stabilizing by effecting compression or tension in the symphysis (see A^2 and A^3 axes in Fig. 7). The role of the TV V in the carp appears to be analogous to that of the transversus mandibularis muscle in the rat (Beecher, '79) in reducing the loading of the symphysis. The long symphysis in the carp, in comparison with most other cyprinids, may emphasize the large forces applied in this fish.

Differentiation and regulation of masticatory activities

Direct and indirect masticatory muscles

The different roles of the masticatory muscles are analogous to those of the direct and indirect flight muscles of insects: Muscles directly attached to the bony (chitinous) elements steer the movement, and the power is supplied indirectly by body muscles. Among steering muscles a further differentiation is made. The LAB V and ROPI still add significant power, as appears from their weight. In addition, the

LAB V and PCIP have a conspicuous role in transmitting forces from the body muscles to the pharyngeal bones. Other direct masticatory muscles, and especially the ROPS, rather stabilize and steer. Free recovery movements of the unloaded pharyngeal bone are achieved by the PCE; this muscle counteracts a multiplicity of movement components and functions as a prime antagonist in pharyngeal mastication. Masticatory movements are guided passively also by Baudelot's ligaments. A comparison of the fiber types in the pharyngeal bone, head, and body muscles in relation to their different roles in mastication is made (Akster and Sibbing, in press).

The time sequence in recruitment of the masticatory muscles in crushing and grinding shows a stable pattern and is independent of the particle size and the type of food (Figs. 9, 15). The duration of the cycle is negatively related, and the forces generated (as judged from the EMG amplitude) are positively related, to the intensity of crushing and grinding. The ability to chew various foods is determined by the multifunctional structure of the occlusal surfaces (Fig. 19) and by the two preprogrammed activity patterns rather than by drastic changes in these patterns. The experiments do provide examples of detailed neural regulation within a masticatory cycle. The balancing of activities between antagonistic muscles functions to improve the masticatory efficiency by maintaining a critical pressure that needs not be higher than required by the materials and must be instantly reduced when fracturing is reached. Transition from crushing into grinding, balancing of antagonistic activities, and instantaneous adjustments to the food (Fig. 15) thus are the active modulations in the stereotyped pattern.

The intensity and duration of the masticatory sequence should be regulated by sensory information; mastication of worms lasts only seconds, whereas chewing of barley lasts minutes. Regulation is mediated by the nervus vagus innervating all pharyngeal bone muscles. Proprioceptive reflex chains, similar to those demonstrated for respiration in the carp by Ballintijn ('72), may include pressure receptors; these are expected to be present, for example, in the connective tissue between chewing pad and the basioccipital process. Sensors in the ROPI muscles or in Baudelot's ligaments might trigger the initiation of the grinding pattern.

Experiments in which the fish accidently fails to bring a large food pellet between teeth and chewing pad reveal some of the normal regulatory mechanism. The LAB V and SRC muscles are not activated (Fig. 13), as would be expected in a normal cycle, and the activity in the PCE muscles is prolonged; adduction of the pharyngeal bones does not start. Apparently, proprioceptive information prevents a normal continuation of the cycle. Lifting of the skull takes place, however, as if crushing were to follow. The powerful indirect masticatory muscles, innervated by spinal nerves, appear more distantly involved and continue their preprogrammed activity once this has been initiated.

Interaction of mastication with food transport, respiration, and other functions in the head

It has been postulated that "the pharyngeal mechanism moves independently of the surrounding cavity" (Gosline, '77:334) and that mastication "need not interrupt respiration" (Alexander, '67:108), since the pharyngeal teeth in the carp lie posterior to the gills. However, it is clear that mastication and respiration are intimately coupled; they permit and even support each other. The kinetics of mastication dominate respiration (Figs. 10, 11e, 16).

During grinding, the vertical buccopharyngeal expansion largely results from the lifting of the skull; during hyperventilation the expansion is equally large but is mainly caused by depression of the pharyngeal floor. The latter consists of multiple components and permits a more accurately adjusted flow of water along the buccopharynx than movements of the rigid skull could provide. Large volume changes are considered to be more a consequence than an aim in mastication.

The frequency of masticatory movements in the carp is about equal to the frequency of respiration and probably is triggered by a similar central generating center. The functional coupling between these two processes in the carp may have been facilitated by the common origin of respiratory and masticatory elements in the branchial arches.

Transport of food to the pharyngeal teeth and esophagus is effected by different mechanisms (see Results, Fig. 17). Food is sucked in with water and trapped between the pharyngeal pads, which act like a muscular tongue and propel it caudad to the teeth. No teeth occur in the anterior buccopharynx. The repetitive movements of the pharyngeal floor probably act in gustation, selecting and cleaning the food. The transport of food from the teeth to the esophagus, deglutition, is effected by the constrictor pharyngis aided by the pharyngeal bone muscles; this was not previously recorded and depicted in fishes.

Cardiac function and pharyngeal bone movements may well be coupled, as the horizontal limbs form the pericardial roof. Furthermore, the proximity of the Weberian ossicles "impose even greater than usual restriction on the flexibility between head and anterior vertebrae" (Gosline, '77:332). The Weberian ossicles, however, almost coincide with the rotation center of the skull and this minimizes their movement. The chain-like arrangement of the ossicles will be a necessity allowing skull movements during mastication and yet maintaining a connection between perilymph and swimbladder. The position of the os suspensorium (Fig. 1) and the attached swimbladder prevents a further caudad extension of the basioccipital pharyngeal process and thus restricts the area of attachment for the ROPI muscles. The laterad movements of the molars against the chewing pad might be seen as a lengthening of the effective grinding stroke, given this restriction in space of the pharyngeal apparatus.

Thus the localization of the masticatory apparatus among those for respiration, hearing, and blood transport in the structural pattern of the head necessitates their functional and structural coordination during evolution.

Pharyngeal mastication in cyprinids and higher teleosts

It is assumed that the buccopharyngeal cavity was primitively covered by numerous small tooth plates that functioned in seizing and swallowing large prey. Fusion subsequently led to enlarged tooth plates in areas of particular functional significance such as jaws, basibranchials, and the posterior gill arches (Nelson, '69). In lower teleosts a grasping type of dentition that includes separate upper pharyngeal tooth plates 4 and 5 seems to be normal. Subsequently, in higher teleosts, tooth plates fused to the gill arch elements and the dentition specialized (Nelson, '69). This trend resulted in a single pair of toothed areas, mainly the infrapharyngobranchials 3, which were equipped with *retractores arcuum branchialium* muscles, typical for all higher teleosts (Neoteleosts; Rosen, '73).

However, some Ostariophysi deviated from the general lower teleostean pattern (Nelson, '69). The pharyngeal jaw system in cyprinids, for example, is highly advanced and toothed upper pharyngeals are completely lacking. Retractor muscles, commonly absent in lower teleosts, insert on the lower pharyngeals. These muscles are not homologous to the retractors found in higher teleosts (Holstvoogd, '65; Rosen, '73).

Liem and Greenwood ('81) recently treated pharyngeal jaws in several acanthopterygian assemblages. The pharyngeal jaw system in the carp, a lower teleost, is based on a structural and mechanical pattern that differs widely from systems found in cichlids, embiotocids, labrids, odacids, and scarids, and is at least as specialized. This is concluded from the following comparison:

1. The shift of the insertion of the major levator components from the upper to the lower pharyngeal jaw is considered a key adaptation in the higher teleosts mentioned above (Liem, '73; Liem and Greenwood, '81). In the carp the huge subtemporal fossae contain bulky levator muscles that attach directly to the lower pharyngeal jaw. In addition, these muscles transmit forces of the epaxial body muscles to the lower pharyngeal jaw. Retractor muscles are inserted on the lower pharyngeals also.
2. The absence of upper pharyngeal jaws in cyprinids and the presence, instead, of a fixed chewing pad supported by the skull allows the recruitment of power from epaxial and hypaxial body muscles for pharyngeal mastication. Summation of these indirect forces with those of the direct pharyngeal bone muscles effects a large load increase on the occlusal surfaces.
3. The muscular sling characterizes the suspension of the pharyngeal jaws in *Embiotocidae* and *Cichlidae*, whereas the lower pharyngeal jaw has been transformed into a lever that articulates with the cleithrum in *Labridae* (Liem, '78; Liem and Greenwood, '81). In the carp both characters are found. The muscular sling is kept in constant tension during crushing, and in the grinding phase of the power stroke muscles rotate the pharyngeal bone as a lever with the ligament of Baudelot as the fulcrum. In this way crushing is transformed into grinding. Thus, fine control, versatility, force, and stabilization are combined effectively.
4. The lack of upper pharyngeal jaws, which perform intrinsic movements and function in mastication as well as food transport in higher teleosts, seems to be compensated by the movable symphysis and intrinsic musculature between the lower pharyngeals in the carp and by the thick pharyngeal pad, which acts as a muscular tongue. These features do not occur in the higher teleosts mentioned.

These characters render the pharyngeal jaw apparatus of the carp both versatile and extremely powerful and, owing to the heterodont dentition, suited for comminution of a variety of food items. The retention of three rows of pharyngeal teeth, considered a primitive character in cyprinids (Chu, '35; Vasnecov, '39; Hensel, '70), and the occlusion exclusively with the chewing pad, enlarge the grinding area in this specialized cyprinid.

From a functional point of view there appears to be a close association between the specialized pipette system of feeding, the development of the pharyngeal jaws, the loss of teeth in the jaws, and the development of premaxillary protrusion in cyprinids (Gosline, '73). The unique combination of these specializations may well have contributed to the development of the cyprinids as the largest family of freshwater fishes.

Catastomids resemble cyprinids to a great extent. The palatal organ is even more developed in catastomids; this is related to its prominent role in gustation, selection, and separation of organic and anorganic food items in these bottom-feeders (Eastman, '77). They, however, lack a chewing pad, except for two mollusc-crushing species, and effective mastication of food against the soft palatal organ will hardly be possible. Pharyngeal teeth are supposed to manipulate, strain, and masticate the food (Eastman, '77).

Among cyprinids a broad spectrum of anatomical features and dietary characteristics is found. Howes ('81) defines a squaliobarbine group of cyprinids involving apomorph characters that lie for the most part in the occipital region of the skull, and he relates them to the increased evolutionary development of the levator of the lower pharyngeal jaw. Following this author, these specializations could be associated with the essentially phytophagous habits of the squaliobarbine taxa. A functional analysis is in progress of pharyngeal mastication in the grasscarp, *Ctenopharyngodon*, a member of this squaliobarbine group that has teeth that, unlike the carp, interdigitate from left and right. Such analyses improve the definition of character complexes belonging to the masticatory system. They also provide a better view on parallel developments in its evolution. This will enhance the tracing of interrelationships between the diversified cyprinid taxa. The present paper demonstrates that the complex of structures involved in mastication extends, at least in carp, far beyond the pharyngeal bones and teeth.

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General summary

The process of food handling in the common carp (*Cyprinus carpio* L.) and its structures associated with feeding are analyzed. The aim of this study is to explain the relation between the the architecture of the head and its functions in food processing and to determine the specializations for some food types and the consequent restrictions for others. Such information improves our understanding of the trophic interrelations between different fish species living together in one community.

- Cyprinids possess pharyngeal jaws, which are modified fifth branchial arches. These are moved by the modified branchial arch muscles against a horny chewing pad in the skull. Oral teeth and a stomach are absent. The upper jaws are protrusile and so aid in the formation of a round suction mouth. The oral and opercular cavity are highly variable in volume. The pharynx is almost fully occupied by the dorsal palatal organ. The pharyngeal floor is composed of the postlingual organ and the branchial sieve. Fibre systems of striated muscles form the bulk of these organs. The branchial arches bear numerous gill rakers. The surface of the pharyngeal roof and floor is almost fully covered by taste buds (up to $820/mm^2$) and mucous cells. The medullar nervous centre of these organs is of about equal size as the forebrain. The narrow slit-like space between both organs has a restricted capacity for volume change, contrary to the situation in most other fishes.
- The role which these structures perform during food uptake and processing in the carp was investigated using cine- and X-ray filming techniques and by synchronously recording the electromyograms of the involved muscles (9 channels). The morphology was studied on the macroscopical and on light- and electron-microscopical level. Food types included commercial fish pellets, barley, earthworms, tubifex, cladocerans and tubifex-soil mixtures. $BaSO_4$-impregnated food was used to follow its path in the X-ray movies.
- Each feeding process is composed of a variable number of stereotyped movement patterns, viz: particulate intake and gulping, selection between food and non-food material (through rinsing, repositioning and backwashing), recollection from the branchial sieve followed by food transport and filling of the chewing cavity, crushing, grinding and deglutition. Probing of the soil and spitting are considered separately.
- The timing, amplitude and velocity of mouth opening, protrusion of the upper jaws, opening of the opercular valve and of the volume changes in the oral,

buccal, pharyngeal and opercular cavities determine the effects of each single pattern. Food intake, selection, transport and mastication impose different demands on the head and can not be combined effectively.

- Different food types are processed in sequences of movement patterns varying in frequency and type according to the specific size, consistency and soilure of the food. Handling times are read from the electromyograms and may differ widely.
- The quantitative distribution pattern of taste buds, mucous cells, club cells and muscle fibers over the oro-pharyngeal surface is measured. Based on these patterns and on other structural characters six areas are distinguished in the oro-pharynx and related with the functions of the above movement patterns for food intake and processing. Scanning E.M. pictures are presented of the common epithelial cells with microridges, cornified cells, mucous cells, taste buds and sensory (?) oligovillous cells.
- Particulate intake is accomplished by fast and voluminous suction, caused by expansion of the orobuccal and opercular cavities. The upper jaws are protruded to produce a fast suction flow (>60 cm/sec), aimed to the particle.

  Gulping, the slow and less aimed uptake of a mouthful of water with suspended foodparticles is accomplished by size increase of the oral cavity mainly. The carp finally encloses the suspension by protruding its upper jaws downward. Oral compression drives the water and food particles over the branchial sieve. The energy required for each gulp will most probably be considerably less than that needed for particulate intake.
- High densities of club cells, which produce the cyprinid alarming substance in the skin, also occur in the orobuccal lining. Their alarming function in this area is doubted.
- Selection between food and non-food requires the retention of edible particles and the expulsion of waste. The electromyograms and electrical stimulations indicate that this separation is achieved by momentary bulgings on the palatal organ, fixing edible particles between pharyngeal roof and floor. Waste particles are flushed through the branchial slits. The complex structure of the palatal organ, the almost maximal densities of taste buds and the cyto-architecture of its regulatory centre in the hindbrain suggest a high level of discrimination in this selection process. The slit-shaped pharynx guarantees a large contact area for selection, but limits its role in suction.
- Protrusion of the upper jaws with the mouth closed plays a crucial role in selection by resuspending food and non-food in the expanding oral cavity. Alternative expansion and compression of the oral cavity creates a for- and backward flow

through the pharyngeal slit and the branchial sieve. Repetition of such 'closed protrusions' and selection effects are graded increasing purification. Closed protrusion movements also serve for merely repositioning of large particles and for recollection of the filtrate from the branchial sieve.

- Cells producing low-viscosity mucus (sialomucines) are found rostrally in the oro-pharynx. It probably serves in lowering the resistance of the wall for the flow of water and in protection of the underlying tissue.

  Cells producing large quantities of highly viscous mucus (sulfomucines) are found in regions were aggregation and clustering of food particles prior to transport is expected.
- Transport of food enveloped in mucus is effected by a peristaltic type of movement in the palatal and postlingual organs. These also propel the food into the chewing cavity being enlarged by depression of the pharyngeal jaws.
- The pharyngeal jaws are suspended in muscular slings from the caudal part of the skull and pectoral girdle. Except an antero-ventral gliding joint with the branchial basket no articulations are present. The symphysis of the jaws allows intrinsic movements. Food is crushed and ground between the pharyngeal teeth and a cornified chewing pad, fixed to the base of the skull. Mastication of grains of maize produces distinct sounds, even distinct close to the experimental tank.
- The epaxial muscles of the carp contribute through rotation of the skull high forces to crushing and grinding. The hypaxial muscles transfer their forces to the pharyngeal teeth by retraction of the pectoral girdle, which provides a large moment-arm. The pharyngeal masticatory apparatus is built for producing and resisting high forces.
- Contrary to these 'power muscles', the hypertrophied pharyngeal jaw muscles act more like 'steering muscles'. They direct and stabilize the pharyngeal jaw movements around four anatomical rotational axes.
- The chewing construction with the rotating skull renders a single Weberian ossicle connecting the sound receiving swimming bladder and the internal ear inside the skull almost impossible. The chain of Weberian ossicles running close to the rotation centre of the skull seems to be a constructive necessity.
- Deglutition is accomplished by compression of the chewing cavity. Bulging of the palatal and postlingual organs closes the entrance and thus direct the transport to the esophagus. Movements of the pharyngeal jaws support transport.
- The apparatus for food uptake and food processing of the carp appears to be specialized to deal with medium-sized and hard food particles (e.g. seeds and shelled mollusks), from 250 µm to about 3% of its standard body length, but also for food items mixed with unedible material. These specializations for

bottomfeeding are most likely basic to the present wide distribution of the common carp and facilitate fish farming.
Large, fast and struggling preys as well as large and flat plant material can hardly be utilized by the carp. Thus, also this 'omnivorous' fish is limited by its specializations in the utilization of the available food items in its environment.

- A tentative scheme relates characters from different parts of the head and unique to the cyprinid family in a functional and structural context. The development of the masticatory apparatus may well have been a key adaptation in the origin of the cyprinid feeding mechanism.
- The present research of the carp provides a new and detailed startingpoint for investigation of the regulatory mechanisms in feeding and for comparisons with native cyprinids like bream roach, tench etc. Knowledge of abilities and restrictions of their structural specializations associated with feeding eludidates which plasticity the fish has to utilize different types of food. This plasticity is a crucial factor for the survival of the species in conditions of food scarcity and co-determines its position in competition. The obtained knowledge thus aids in predicting the effects of environmental changes on the trophic interactions and composition of the fish fauna.

Curriculum vitae.

Nand Sibbing werd op 16 december 1946 te 's-Gravenhage geboren. Verrijkt met een solide onderbouw op de kleuterschool, werd de St.Vincentius school doorlopen, daarmee een aaneensluitende periode van 25 jaar lager onderwijs aan ons gezin volmakend. De brede en stimulerende vorming op het Aloysius college werd in 1966 met het diploma gymnasium β afgesloten. De cijfers voor de klassieke talen op mijn examenlijst doen niet vermoeden hoezeer zij mij soms dwarslagen.

Het kandidaatsexamen biologie (B3; hoofdvak biofysika) werd in 1969 aan de rijksuniversiteit te Leiden behaald. De Australische regering stelde mij daarna met enkele andere studenten in staat drie maanden stage te lopen in de immunologie (Walter & Eliza Hall Institute, Melbourne) en zo het land (en mijn broers en zuster daar) beter te leren kennen. Afgewisseld met praktikum-assistentschappen werden drie onderwerpen in mijn doktoraalstudie bewerkt:

1) Funktionele morfologie van het kauwapparaat bij de karper (dr. J.W.M. Osse, Zool. Lab. Leiden). Dit onderwerp wormde de eerste aanzet tot dit proefschrift.
2) Cytochrome b-6 reacties in *Porphyridium aerugineum* (dr. J. Amesz, Lab. voor Biofysika, Leiden).
3) Funktionele verschillen tussen het oog van de gele aal en de zilveraal *(Aguilla anguilla* L.) en de betekenis van deze verschillen voor de migratie van de zilveraal. (dr. F.J. Verheijen, Lab. Verg. Fysiologie, Utrecht).

Het doctoraalexamen biologie werd in januari 1973 (cum laude) behaald. De onderwijsbevoegdheid aantekening bleef steken op de hospiteerstages, die door mijn tewerkstelling aan de Landbouwhogeschool te Wageningen niet meer konden worden vervuld.

Sinds maart 1973 ben ik als wetenschappelijk medewerker aangesteld bij de Vakgroep Experimentele Diermorfologie en Celbiologie (toen nog Dierkunde geheten). De eerste drie jaren werden geïnvesteerd in de organisatie en opbouw van het biologie onderwijs. Het onderzoek kreeg hierna geleidelijk meer ruimte en leidde tot de bewerking van dit proefschrift. Taken in onderwijs, organisatie en beheer vormen nog steeds een belangrijk bestanddeel.